The

AMERICAN MIDLAND NATURALIST

Founded by
J. A. NIEUWLAND, C.S.C.

Vol. 66 October, 1961 No. 2

Published by
THE UNIVERSITY OF NOTRE DAME
Notre Dame, Indiana

Contents

An Annotated List of Fishes from the Coosa River System of Alabama ..... Herbert Boschung 257

Phenology of Sumacs ..... Elizabeth F. Gilbert 286

Habitat Selection and Activity of the Wood Frog, Rana sylvatica Le Conte ..... Harold Heatwole 301

The Site of Udonella caligorum (Trematoda) Upon Parasitic Copepod Hosts ..... David Causey 314

The Genus Naematelia ..... Robert J. Bandoni 319

Comments on the Mayfly Genus Campylocia with a Description of a New Species (Euthyplociidae: Euthyplociinae) ..... Lewis Berner and T. B. Thew 329

Cyprinid Fishes of the Subgenus Cyprinella of Notropis. IV The Notropis galacturus-camurus Complex ..... R. H. Gibbs, Jr. 337

Mycological Notes II. New Taxa, Synonyms, and Records ..... Marie L. Farr 355

Studies on the Biology of Philophthalmus gralli Mathis and Leger, 1910 (Trematoda: Digenea) ..... Fred A. West 363

Life History of the Pigmy Salamander, Desmognathus wrighti, in Virginia ..... James A. Organ 384

A New Species of Echinostelium from Greece ..... C. J. Alexopoulos 391

A Synopsis of Pinguicula (Lentibulariaceae) in the Southeastern United States ..... R. K. Godfrey and H. Larry Stripling 395

Morphological Variation Between Local Populations of Taricha granulosa in Oregon ..... Robert L. Livezey & Gilbert A. Wyllie 410

Forest History of Martha's Vineyard, Massachusetts 1. Modern and Pre-Colonial Forests ..... J. Gordon Ogden 417

The Red Eye Pigment Determination in the Drosophila affinis subgroup ..... Bill W. Geer 431

Laboratory Life History of the Eastern Harvest Mouse ..... Stephen V. Kaye 439

Occurrence of Subterranean Isopods in Epigean Waters ..... W. L. Minckley 452

A New Genus of Fossil Salamander from North America ..... Walter Auffenberg 456

Liatris provincialis, sp. nov., (Compositae), Endemic in Western Florida ..... R. K. Godfrey 466

Observations on Fleas (Siphonaptera) of Some Small Mammals in Northwestern Illinois ..... B. J. Verts 471

Wintering Distribution Changes in Mallards and Black Ducks ..... Paul A. Johnsgard 477

The Effects of Fire in the Okefenokee Swamp in 1954 and 1955 ..... Eugene Cypert 485

Notes and Discussion

An Interesting Growth Relationship Between Two Specimens of Erythrina sandwicensis ..... B. J. Britten 504

Book Reviews 505

ROBERT E. GORDON
Editor

Executive Committee

ROBERT P. McINTOSH — RALPH E. THORSON
JOSEPH A. TIHEN — KENYON S. TWEEDELL

BOARD OF ASSOCIATE EDITORS

ROLLIN H. BAKER.....*Mammalogy*
B. D. BURKS.....*Entomology*
ELON E. BYRD.....*Parasitology*
FRED R. CAGLE.....*Herpetology*
ALBERT L. DELISLE.....*Plant Morphology*
THEODOSIUS DOBZHANSKY.....*Genetics and Cytology*
CARROLL LANE FENTON.....*Invertebrate Paleontology*
DAVID G. FREY.....*Animal Ecology*
R. K. GODFREY.....*Systematic Botany*
THEODORE L. JAHN.....*General Physiology*
PAUL J. KRAMER.....*Plant Physiology*
JEAN MYRON LINSDALE.....*Ornithology*
W. GARDNER LYNN.....*Embryology*
GEORGE WILLARD MARTIN.....*Mycology*
CALVIN McMILLAN.....*Plant Ecology*
ROBERT W. PENNAK.....*Invertebrate Zoology*
LOREN P. WOODS.....*Ichthyology*

THE AMERICAN MIDLAND NATURALIST is a general biological periodical published quarterly by the University of Notre Dame. It welcomes to its pages articles of a descriptive, analytical, and experimental nature. Review articles on topics of current interest in the various fields of Biology are also welcome.

Subscription rate per year $10.00 in the U.S., Mexico, and South American countries; $11.00 elsewhere.

Address All Correspondence to:

AMERICAN MIDLAND NATURALIST
University of Notre Dame
Notre Dame, Indiana

© 1961, University of Notre Dame Press.

Entered as second-class matter at Notre Dame, Indiana. Accepted for mailing at special rate of postage provided for in Section 1103; Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 66 OCTOBER, 1961 No. 2

An Annotated List of Fishes from the Coosa River System of Alabama[1]

HERBERT T. BOSCHUNG, JR.

Department of Biology, University of Alabama

ABSTRACT: A survey of the fish fauna of the Coosa River drainage, a major tributary of the Alabama system, was conducted in June, 1959. Collections were made at 44 stations. The results of these and 10 collections made in previous years, plus records from the literature, show the fish fauna of the Coosa drainage of Georgia and Alabama to comprise 20 families and 85 species. Ten species are endemic to the upper Alabama system, and 10 represent new records for the Coosa drainage. Each collecting station is described and the species collected are listed. Annotations include notes on the morphology, color, and ecology of many of the species. The number of specimens collected at each station, and the size ranges are given for each species. A bibliography for each species is also included.

The Coosa River is formed by the confluence of the Etowah and Oostanaula rivers at Rome, Georgia. It flows in a southwesterly direction almost to Montgomery, Alabama where it joins with the Tallapoosa to form the Alabama. The Alabama River meets the Tombigbee to form the Mobile, the largest Gulf drainage east of the Mississippi.

The purpose of this paper is to present data on the presence and distribution of the fishes of the Coosa River system which, along with similar data from other southeastern streams, will eventually result in establishing zoogeographic patterns, and which will contribute to our understanding of the divergence of the upper Mobile basin fish fauna from that of the Tennessee from which it presumably originated.

The first paper on the fishes of the Coosa River system was published by David Starr Jordan in 1877. Jordan listed 56 species from tributaries of the Etowah and Oostanaula Rivers in the vicinity of Rome, Georgia. Forty-six of Jordan's fishes are recognized as valid species. Twelve of the 13 species he described as new are recognized as valid species today. Jordan and Brayton (1878) expanded this list to include the entire Alabama basin and added one species to the list of known fishes of the Coosa River. In another paper, Jordan (1879) listed fishes from the Etowah River. Gilbert's (1891) report was the first to include fishes from the Coosa River of Alabama. Fowler's (1945) records are from Dekalb and Cherokee Counties, Alabama,

[1] This project was supported by a grant from the University of Alabama Research Committee.

and Scott's (1951) are from the Coosa River near Childersburg, Alabama. These and all other literature records of fishes of the Coosa River system known to the author are included in the synonymies. Based on these data and those obtained as a result of this research, 84 species are definitely known to occur in the Coosa River system, plus those listed herein as probable or doubtful.

Acknowledgments.—I wish to acknowledge the assistance of Robert E. Smith in collecting the material for this paper, and the encouragement and advice from Ralph L. Chermock during the writing of the report. Appreciation is also due Royal D. Suttkus for identifying specimens of *Notropis bellus* and *N. lirus*, along with several darters, including an apparently unnamed species in the subgenus *Ulcocentra*.

MATERIALS AND METHODS

In June, 1959, Robert E. Smith and I collected in the Coosa drainage of Alabama as part of a continuing survey of the fish fauna of the Mobile basin conducted by the University of Alabama. Ten collections from the Coosa were made in previous years; to these, we add 44 more stations. These are numbered in sequence from north to south (Figure 1). Each station was thoroughly sampled until the collectors were convinced that subsequent trials would probably not yield additional species. Dissolved oxygen was determined by the Alsterberg (Azide) modification of the Winkler method as described by Lagler (1956). Counts and measurements were made according to the method of Hubbs and Lagler (1947).

The following abbreviations are used in addition to the standard compass directions: T = townships, R = range, sec. = section, elev. = elevation, C = centigrade, ppm = parts per million, mm = millimeters, Co. = County, R= River, Cr. = Creek, trib. = tributary, UAIC = University of Alabama Ichthyological Collection (the Accession Number follows).

The number of specimens and the range of total length in millimeters are indicated in parentheses following the station number in the annotated list. For example, (12, 52-68) means 12 specimens ranging from 52 to 68 millimeters in total length. Ranges, townships, sections, and elevations were determined from U. S. Geological Survey Maps (AMS series), scale 1: 250,000. Elevations are given in contour intervals of 100 feet above 1000 foot elevations and in intervals of 50 feet below 1000 foot elevations.

COLLECTION STATIONS IN THE COOSA RIVER DRAINAGE OF ALABAMA

Station 1. West Fork Little River, T 6 S, R 10 E, sec. 19; elev. 1500 feet; Desoto State Park, 7 miles south of Mentone, Dekalb Co., June 4, 1959. Water clear; current moderate to fast; bottom bed rock; depth 3 feet; width 30 feet. Water temperature 19.5°C; dissolved

oxygen 8.8 ppm. Method of capture: cast net. UAIC 632. Species[2]: 31.

Station 2. A branch tributary to West Fork Little River, T 6 S, R 10 E, sec. 30; elev. 1500 feet; 8 miles south of Mentone, Dekalb Co., June 4, 1959. Water clear; current still to moderate; bottom mud; depth 1 foot; width 12 feet. Water temperature 17°C; dissolved oxygen 8.5 ppm. Method of capture: seine. UAIC 633. Species: 24 and 67.

Station 3. Little River, T 7 S, R 10 E, sec. 30; elev. 1200 feet; 2.5 miles north of Blanche, on Cherokee-Dekalb Co. line, June 4, 1959. Water clear; current moderate to swift, with still pools above water fall; bottom bed rock. Collections were made with cast net in pools near shore. UAIC 674. Species: 62.

Station 4. Sells' Cave, T 9 S, R 7 E, sec. 4; elev. 700 feet; 3 miles west of Collinsville, Dekalb Co., June 29, 1958. Water crystal clear. Water temperature 14°C. Water depth at entrance of cave approximately 10 feet. Water is not known to flow from the cave. Big Wills Creek is about 400 feet south of the cave at an elevation of 650 feet. Collectors: Robert E. Smith, Jesse White and Herbert Boschung. Method of capture: dip net. UAIC 656. Species: 53.

Station 5. Little Creek, tributary of Big Wills Creek, T 9 S, R 7 E, sec. 8; elev. 700 feet; 3.5 miles west of Collinsville, Dekalb Co., June 3, 1959. Water turbid following rain; current moderate to fast; bottom mostly gravel, some soft clay; depth 1.5 feet; width 10 feet. Water temperature 20°C; dissolved oxygen 8.5 ppm. Method of capture: seine. UAIC 631. Species: 22, 24, 36, 62, and 81.

Station 6. Big Wills Creek, 10 miles northeast of Attalla, Etowah Co., June 5, 1953. Water turbid; current swift; bottom sand, rock and mud; width to 30 feet. Water temperature 18°C. Collector: L. B. Cooper. Method of capture: seine. UAIC 477. Species: 27, 74, 78, and 85.

Station 7. Clear Creek, tributary of Big Wills Creek, 5 miles northeast of Gallant, Etowah Co., July 27, 1955. Water clear; width 15 feet. Collector: Henry Howell. Method of capture: seine. UAIC 457. Species: 22, 24, 35, 36, 37, 45, 54, 78, 81, and 85.

Station 8. Big Wills Creek, 5 miles west of Gadsden, Etowah Co., June 5, 1953. Water turbid; current swift; bottom rock, sand and mud; depth to 4 feet; width to 40 feet. Water temperature 22°C. Collector: L. B. Cooper. Method of capture: seine. UAIC 476. Species: 16, 67, and 68.

Station 9. Nances Creek, T 14 S, R 9 E, sec. 2; elev. 900 feet; 6.5 miles north of White Plains, Calhoun Co., June 5, 1959. Water slightly turbid; current moderate to swift; bottom silt and rock; depth 1 foot; width 12 feet. Water temperature 19°C; dissolved oxygen 8.5 ppm. Method of capture: seine; cast net. UAIC 634. Species: 22, 24, 31, 35, 45, 62, 64, 75, 78, and 81.

---

[2] The numbers refer to the annotated list of species to follow.

Station 10. Nances Creek, T 12 S, R 10 E, sec. 33; elev. 600 feet; one mile northeast of Piedmont, Calhoun Co., July 23, 1949. Collector: Ben Sanders. Method of capture: seine. UAIC 36. Species: 22.

Station 11. Terrapin Creek, T 12 S, R 10 E, sec. 27; elev. 650 feet; 3 miles northeast of Piedmont, Cherokee-Calhoun Co. line, July 9, 1949. Collector: Ben Sanders. Method of capture: seine. UAIC 37. Species: 22 and 30.

Station 12. Terrapin Creek, T 11 S, R 10 E, sec. 20; elev. 600 feet; Coloma, Cherokee Co., June 4, 1959. Water moderately muddy; current slow; bottom clay and gravel; depth 1 foot; width 10 feet. Method of capture: seine. UAIC 675. Species: 56.

Station 13. Little Canoe Creek, T 12 S, R 4 E, sec. 21; elev. 800 feet; 2 miles south of Gallant. Etowah-St. Clair Co. line, July 29, 1955. Collector: Henry Howell. Method of capture: seine. UAIC 459. Species: 35, 67, 68, and 81.

Station 14. Little Canoe Creek, T 12 S, R 4 E, sec. 25; elev. 800 feet; 2.5 miles northeast of Steele, Etowah-St. Clair Co. line, July 28, 1955. Collector: Henry Howell. Method of capture: seine. UAIC 458. Species: 17, 27, 28, 35, 37, 39, 45, 61, 67, 68 and 81.

Station 15. Big Canoe Creek T 14 S, R 2 E, sec. 13; elev. 900 feet; one mile east of Caldwell, St. Clair Co., June 15, 1959. Water turbid; depth 8 feet, width 30 feet. Method of capture: cast net. UAIC 649. Species: 16, 29, 55, 66, and 68.

Station 16. South Fork of Big Canoe Creek, T 15 S, R 1 E, sec. 1; elev. 900 feet; 2 miles west of Springville, St. Clair Co., June 15, 1959. Water clear; current slow to moderate; bottom small rock and gravel; depth 1.5 feet; width 8 feet. Water temperature 19.5°C; dissolved oxygen 8.4 ppm. Method of capture: seine; cast net. UAIC 648. Species: 16, 22, 31, 33, 36, 37, 41, 45, 54, 55, 68, and 81.

Station 17. Big Canoe Creek, T 14 S, R 4 E, sec. 6; elev. 900 feet; one mile east of Ashville, St. Clair Co., June 15, 1959. Water turbid; current slow to moderate; bottom mud; depth 3 feet; width 20 feet. Method of capture: cast net. UAIC 650. Species: 29, 30, and 68.

Station 18. Permeter Creek, T 13 S, R 5 E, sec. 34; elev. 600 feet; 2 miles northwest of Greensport, St. Clair Co., June 16, 1959. Water slightly muddy; current slow; bottom mud; depth 3 feet; width 20 feet. Water temperature 21°C; dissolved oxygen 7.5. Method of capture: cast net. UAIC 652. Species: 37, 41, 55, 56, 66, 67, 68, and 71.

Station 19. Near mouth of Beaver Creek, T 14 S, R 5 E, sec. 1; elev. 600 feet; Greensport, St. Clair Co., June 16, 1959. Water turbid, current slow; bottom mud; depth 5 feet; width 20 feet. Water temperature 20.5°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 651. Species: 28, 31, 33, 37, 39, 41, 45, 56, 67, and 68.

Station 20. Near mouth of Shoal Creek, T 14 S, R 5 E, sec. 13;

elev. 600 feet; 2 miles south of Greensport, St. Clair Co., June 16, 1959. Water slightly muddy; current moderate; bottom rocky; depth 1.5 feet; width 20 feet. Water temperature 21°C; dissolved oxygen 7.8 ppm. Method of capture: seine; cast net. UAIC 653. Species: 16, 22, 28, 29, 30, 31, 33, 41, 45, and 68.

Station 21. Near mouth of Bridge Creek, T 14 S, R 6 E, sec. 30; elev. 500 feet; 4 miles south of Greensport, St. Clair Co., June 16, 1959. Water muddy; current very slow; bottom mud; depth 5 feet; width 20 feet. Method of capture: cast net. UAIC 654. Species: 74.

Station 22. Broken Arrow Creek, T 16 S, R 4 E, sec. 5; elev. 500 feet; 7.5 miles southwest of Ragland, St. Clair Co., June 16, 1959. Water slightly turbid; current slow to moderate; bottom rock and mud; depth 3 feet; width 20 feet. Water temperature 19.5°C; dissolved oxygen 7.4 ppm. Method of capture: seine; cast net. UAIC 655. Species: 10, 17, 29, 33, 36, 39, 45, 55, 61, 67, 68, 75, and 85.

Station 23. Choccolocco Creek, T 15 S, R 9 E, sec. 22; elev. 700 feet; 1 mile east of Pleasant Ridge, Calhoun Co., June 5, 1959. Water moderately turbid; current still to moderate; bottom silt and mud; depth to 8 feet; width to 60 feet. Water temperature 19.5°C; dissolved oxygen 8.3 ppm. Method of capture: seine; cast net. UAIC 635. Species: 10, 16, 22, 24, 28, 29, 32, 35, 37, 54, 56, 63, 64, 70, and 85.

Station 24. Choccolocco Creek, T 15 S, R 9 E, sec. 27; elev. 700 feet; 1.5 miles north of Iron City, Calhoun Co., June 5, 1959. Water clear; current moderate to swift; bottom gravel and sand; depth 1 foot; width 8 feet. Water temperature 19.5°C; dissolved oxygen 8.5 ppm. Method of capture: seine; cast net. UAIC 636. Species: 22, 31, 35, 36, 45, 54, 62, and 81.

Station 25. Cane Creek, T 15 S, R 8 E, sec. 17; elev. 600 feet; Fort McClellan, Calhoun Co., August 5, 1949. Method of capture: seine. UAIC 46. Species: 45.

Station 26. Cane Creek, T 15 S, R 7 E, sec. 11; elev. 700 feet; 6 miles north of Anniston, Calhoun Co., June 9, 1959. Water moderately turbid; current slow to moderate; bottom mud and gravel; depth 1.5 feet; width 15 feet. Water temperature 21.5°C; dissolved oxygen 7.2 ppm. Method of capture: seine; cast net. UAIC 643. Species: 19, 35, 37, 41, 45, 56, 75, and 85.

Station 27. Chehaw-haw Creek above lake at Cheaha State Park, T 18 S, R 8 E, sec. 8; elev. 1200 feet; Cleburne Co., June 6, 1959. Water clear; current moderate to swift; bottom gravel and rock; depth 1 foot; width 7 feet. Water temperature 19°C; dissolved oxygen 9.0 ppm. Method of capture: seine; cast net. UAIC 638. Species: 24, 31, and 65.

Station 28. Chehaw-haw Creek below lake at Cheaha State Park, T 18 S, R 8 E, sec. 8; elev. 1200 feet; Cleburne Co., June 6, 1959. Water clear; current swift; moderately still pools; bottom gravel and rock; depth 1 foot; width 7 feet. Water temperature

22°C; dissolved oxygen 8.6 ppm. Method of capture: seine; cast net. UAIC 637. Species: 24, 63, 65, and 68.

Station 29. Chehaw-haw Creek, tributary of Lake Chinnabee, T 18 S, R 7 E, sec. 14; elev. 1000 feet; Talladega National Forest, Clay Co., June 8, 1959. Water clear; current moderate; bottom rocky; depth 2 feet; width 15 feet. Water temperature 22°C; dissolved oxygen 7.3 ppm. Method of capture: seine; cast net. UAIC 640. Species: 29, 30, 31, 33, 56, 65, 66, 68, and 85.

Station 30. Cheaha Creek, tributary of Chehaw-haw Creek, T 18 S, R 7 E, sec. 5; elev. 700 feet; 2 miles east of McElderry, Talladega Co., June 8, 1959. Water clear; current moderately swift, with still pools; bottom rock, gravel, sand and mud; depth 1 foot; width 15 feet. Water temperature 24.5°C; dissolved oxygen 7.2 ppm. Method of capture: seine; cast net. UAIC 639. Species: 16, 22, 24, 29, 30, 31, 35, 41, 54, and 68.

Station 31. Chehaw-haw Creek, tributary of Choccolocco Creek, T 18 S, R 6 E, sec. 1; elev. 600 feet; McElderry, Talladega Co., June 9, 1959. Water clear; current slow to moderate; bottom mud, silt and rock; depth 3 feet; width 18 feet. Water temperature 22°C; dissolved oxygen 7.4 ppm. Method of capture: seine; cast net. UAIC 641. Species: 22, 25, 27, 29, 31, 33, 36, 37, 39, 41, 45, 54, 55, 63, 67, 68, and 78.

Station 32. Salt Creek, tributary of Choccolocco Creek, T 17 S, R 7 E, sec. 20; elev. 500 feet; 1.8 miles east of Munford, Talladega Co., June 9, 1959. Water clear to slightly turbid; current slow to moderate; bottom mud, silt, gravel and rock; depth 2 feet; width 20 feet. Water temperature 21°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 642. Species: 16, 22, 24, 29, 37, 39, 45, 63, and 67.

Station 33. Talladega Creek, T 19 S, R 5 E, sec. 5; elev. 500 feet; 3 miles south of Talladega, Talladega Co., June 10, 1959. Water turbid; current moderate; bottom rock, gravel, and coarse sand; depth 2 feet; width 30 feet. Water temperature 22°C; dissolved oxygen 7.9 ppm. Method of capture: cast net. UAIC 644. Species: 16, 18, 22, 27, 29, 37, 39, 45, 67, 68, and 74.

Station 34. Weewoka Creek, T 20 S, R 4 E, sec. 2; elev. 500 feet; Winterboro, Talladega Co., June 10, 1959. Water clear; current slow to moderate; bottom rock and gravel; depth 1 foot; width 15 feet. Water temperature 19.5°C; dissolved oxygen 7.9 ppm. Method of capture: seine; cast net. UAIC 645. Species: 22, 25, 31, 35, 36, 37, 39, 41, 45, and 78.

Station 35. Clear Creek, T 19 S, R 2 E, sec. 15; elev. 500 feet; Vincent, Shelby Co., June 17, 1959. Water clear; current slow to moderate; bottom rock and gravel; depth 1.5 feet; width 20 feet. Water temperature 20°C; dissolved oxygen 7.8 ppm. Method of capture: seine; cast net. UAIC 657. Species: 16, 22, 24, 29, 31, 35, 36, 41, 45, 54, 65, 78, 81, and 85.

Station 36. Coosa River, T 20 S, R 3 E, sec. 18; elev. 450 feet;

one mile northwest of Childersburg on Talladega-Shelby County line, September 13, 1954. Water turbid; shore rock, sand and clay. Collector: Henry Howell. Method of capture: rotenone. UAIC 447. Species: 8, 14, 18, 25, 38, 46, 50, 60, 63, 82, and 84.

Station 37. A nameless creek, one mile from the Coosa River, T 20 S, R 2 E, sec. 15; elev. 450 feet; approximately 2.5 miles east of U. S. Hwy. 280, Shelby Co., June 10, 1959. Water slightly turbid; current slow to moderate; bottom mud; depth 1.5 feet; width 12 feet. Water temperature 24°C; dissolved oxygen 7.6 ppm. Method of capture: cast net. UAIC 646. Species: 23, 24, 29, 38, 45, 56, 62, 63, 67, 68, and 78.

Station 38. Four-mile Creek, T 20 S, R 1 E, sec. 25; elev. 500 feet; 1.5 miles north of Wilsonville, Shelby Co., June 17, 1959. Water clear; current slow to moderate; bottom rock and gravel; depth 1 foot; width 15 feet. Water temperature 22.5°C; dissolved oxygen 7.7 ppm. Method of capture: seine; cast net. UAIC 658. Species: 10, 22, 29, 31, 33, 36, 37, 41, 45, 56, 74, 75, 78, 81, and 88.

Station 39. Beeswax Creek, T 21 S, R 1 E, sec. 8; elev. 500 feet; 4.5 miles northeast of Columbiana, Shelby Co., June 17, 1959. Water slightly turbid; current slow; bottom rock and mud; depth 2 feet; width 10 feet. Water temperature 21°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 659. Species: 11, 17, 19, 33, 37, 41, 62, 64, 67, 68, and 74.

Station 40. Camp Branch of Waxahatchee Creek, T 22 S, R 1 W, sec. 6; elev. 500 feet; 5.5 miles southwest of Columbiana, Shelby Co., June 10, 1959. Water clear; current moderate; bottom rock and gravel; depth 1 foot; width 18 feet. Method of capture: cast net. UAIC 647. Species: 11, 33, 41, 55, 67, 74, and 83.

Station 41. Waxahatchee Creek, T 24 N, R 15 E, sec. 28, elev. 400 feet; 5 miles south of Shelby on Shelby-Chilton Co. line, June 17, 1959. Water clear; current moderate; bottom rock and gravel; depth 1 foot; width 15 feet. Water temperature 19°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 661. Species: 22, 35, 36, 45, 68, and 85.

Station 42. Waxahatchee Creek, T 24 N, R 15 E, sec. 25; elev. 400 feet; backwater of Lay Lake, Shelby Co., June 17, 1959. Water slightly muddy; currently still; bottom clay and gravel. Water temperature 25°C. Method of capture: cast net. UAIC 660. Species: 9, 55, 63, 66, 68, and 74.

Station 43. Channel of Coosa River, T 23 N, R 15 E, sec. 13; elev. 300 feet; 1 mile north of Lay Dam, Chilton Co., June 18, 1959. Water turbid; current still. Method of capture: basket traps in approximately 20 feet of water. UAIC 662. Species: 46 and 47.

Station 44. Yellowleaf Creek, T 23 N, R 15 E, sec. 17; elev. 400 feet; Jumbo, Chilton Co., June 18, 1959. Water clear; current moderate; bottom rock and gravel; depth 1 foot; width 20 feet. Water temperature 22.5°C; dissolved oxygen 8.3 ppm. Method of capture:

seine; cast net. UAIC 663. Species: 17, 29, 33, 35, 36, 37, 39, 40, 55, 63, 67, 74, and 81.

Station 45. Hatchet Creek, T 23 N, R 19 E, sec. 30; elev. 450 feet; 4 miles north of Rockford, Coosa Co., June 19, 1959. Water slightly turbid; current still to moderate; bottom silt and rock; depth 1.5 feet; width to 50 feet. Water temperature 23°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 673. Species: 61 and 67.

Station 46. Swamp Creek, T 21 N, R 18 E, sec. 1; elev. 500 feet; 1.5 miles north of Pantonville, Coosa Co., June 19, 1959. Water slightly turbid; current slow to moderate; both sand and fine gravel; depth 1 foot; width 20 feet. Water temperature 21°C; dissolved oxygen 8.4 ppm. Method of capture: seine; cast net. UAIC 672. Species: 16, 29, 30, 34, and 39.

Station 47. Weoka Creek, T 20 N, R 18 E, sec. 2; elev. 500 feet; 4.5 miles south of Pantonville, on Coosa-Elmore Co. line, June 19, 1959. Water slightly turbid; current still to moderate; bottom silt. Water temperature 22°C. Method of capture: seine and cast net from shore. UAIC 671. Species: 22, 29, 30, 34, 37, 39, and 74.

Station 48. Little Weoka Creek, T 20 N, R 18 E, sec. 11; elev. 500 feet; 6.5 miles north of Riddle, Elmore Co., June 19, 1959. Water slightly turbid; current slow to moderate; bottom rock and gravel; depth 2 feet; width 10 feet. Water temperature 20.5°C; dissolved oxygen 7.5 ppm. Method of capture: cast net. UAIC 670. Species: 25, 29, 34, 37, and 76.

Station 49. Chestnut Creek, T 21 N, R 15 E, sec. 36; elev. 400 feet; Verbena, Chilton Co., June 18, 1959. Water slightly turbid; current moderate; bottom rock, gravel, and clay; depth 1.5 feet; width 30 feet. Water temperature 21°C; dissolved oxygen 8.4 ppm. Method of capture: seine; cast net. UAIC 664. Species: 17, 39, 68, and 74.

Station 50. West Branch of Shoal Creek, T 20 N, R 16 E, sec. 26; elev. 400 feet; 1 mile north of Wadsworth, Autauga Co., June 18, 1959. Water clear; current still to moderate; bottom rock and gravel; depth 1 foot; width 5 feet. Water temperature 21°C; dissolved oxygen 7.7 ppm. Method of capture: cast net. UAIC 665. Species: 22, 34, and 37.

Station 51. Coosa River below Jordan Dam, T 19 N, R 18 E, sec. 22; elev. 200 feet; Elmore Co., June 19, 1959. Water slightly turbid; current moderate to swift. Water temperature 21.5°C; dissolved oxygen 6.6 ppm. Method of capture: cast net from shore and by hook and line. UAIC 667. Species: 4, 6, 7, 8, 38, 46, 52, 55, 58, 59, 61, 66, and 68.

Station 52. Pigeonroost Creek, T 19 N, R 18 E, sec. 34; elev. 200 feet; 3.5 miles northwest of Wetumpka, Elmore Co., June 18, 1959. Water slightly turbid; current slow to moderate; bottom gravel; depth 1.5 feet; width 10 feet. Water temperature 23°C; dissolved

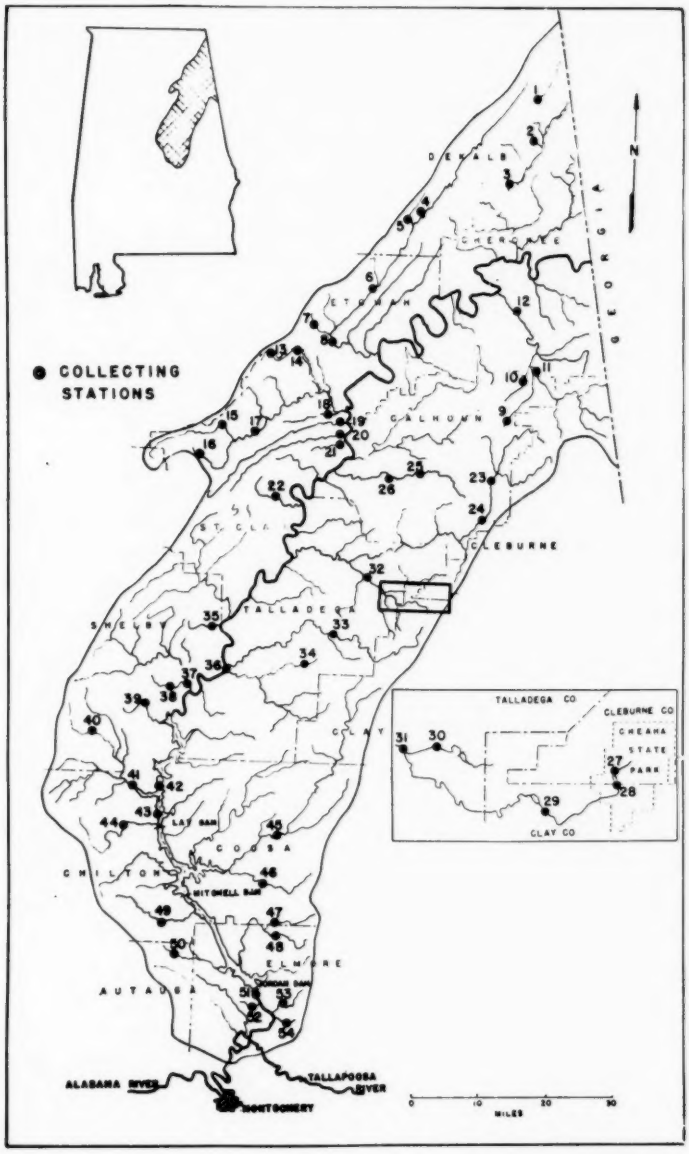


Fig. 1.—The Coosa River drainage of Alabama. The numbered collecting stations are described in the text.

oxygen 5.5 ppm. Method of capture: seine; cast net. UAIC 666. Species: 34, 40, 55, 63, 67, and 74.

Station 53. A nameless creek, T 18 N, R 19 E, sec. 6; elev. 200 feet; on east side of Coosa River, 3 miles north of Wetumpka, Elmore Co., June 19, 1959. Water slightly turbid; current moderate; bottom rock; depth 2 feet; width 25 feet. Water temperature 21.5°C; dissolved oxygen 8.3 ppm. Method of capture: seine; cast net. UAIC 668. Species: 18, 22, 23, 29, 37, 42, 45, 55, 62, 63, 67, and 68.

Station 54. A nameless creek, T 19 N, R 18 E, sec. 25; elev. 200 feet; on east side of Coosa River, 2.5 miles north of Wetumpka, Elmore Co., June 19, 1959. Water clear to slightly turbid; current slow; bottom sand and gravel; depth 1 foot; width 10 feet. Water temperature 21.5°C; dissolved oxygen 7.4 ppm. Method of capture: seine; cast net. UAIC 669. Species: 42 and 65.

ANNOTATED LIST OF SPECIES

PETROMYZONTIDAE—Lampreys

1. *Ichthyomyzon castaneus* Girard

Ichthyomyzon concolor.—Gudger, 1930: 145 (Coosa River, Rome, Ga.).

According to Hubbs and Trautman (1937), Gudger's specimens belong to this species. No new records.

2. *Ichthyomyzon gagei* Hubbs and Trautman.

Two records of this nonparasitic species are known from the Alabama River System. A paratype is from a tributary of the Alabama River in Wilcox Co. (Hubbs and Trautman, 1937), and Dendy and Scott (1953) collected them from several tributaries of the Tallapoosa River in Lee Co., Alabama. Although this lamprey has not been reported from the Coosa drainage, little doubt remains that it occurs there.

3. *Lampetra aepyptera* (Abbott)

Lampetra aepyptera.—Raney, 1952: 99 (tributary of Oostanaula River, Rome, Ga.).

No new records. This lamprey has not been collected from the Coosa drainage of Alabama, but it undoubtedly occurs throughout the Mobile basin. It has been reported by Cook (1952) from the Tombigbee and Pascagoula drainages, and by Cooper and Hemphill (1957) and Smith (1960) from tributaries of the Warrior River.

POLYODONTIDAE—Paddlefishes

4. *Polyodon spathula* (Walbaum)

The paddlefish was not seen by the author; however, a fisherman reported catching 22 "spoonbill cats" below Jordan Dam (station *51*) on the night of June 18, 1959.

ACIPENSERIDAE—Sturgeons

5. *Acipenser fulvescens* Rafinesque

Acipenser fulvescens.—Scott, 1951: 31.

No new records.

LEPISOSTEIDAE—Gars

6. *Lepisosteus osseus* (Linnaeus)

Lepidosteus osseus.—Jordan, 1877a: 369; Jordan and Brayton, 1878: 55; Jordan, 1879: 119.

Lepisosteus osseus.—Scott, 1951: 31.

One specimen measuring approximately 4 feet in total length was captured by hook and line at station *51*.

CLUPEIDAE—Herrings

7. *Alosa chrysochloris* (Rafinesque)

Four specimens varying from 230 to 242 mm in total length were collected with the cast net at station *51*.

8. *Dorosoma cepedianum* (LeSueur)

Dorysoma cepedianum heterurum.—Jordan, 1877a: 368.

Dorosoma cepedianum var. *heterurum.*—Jordan and Brayton, 1878: 49 (Montgomery, Ala.).

Dorosoma cepedianum.—Scott, 1951: 37.

Twelve specimens measuring from 95 to 123 mm were obtained with rotenone at station *36*, and one 212 mm specimen was collected with a cast net at station *51*.

9. *Dorosoma petenense* (Günther)

Four specimens measuring 50 to 56 mm were collected in the backwater of Lay Lake (station *42*).

ESOCIDAE—Pikes

10. *Esox americanus* Gmelin

Esox raveneli.—Jordan, 1877a: 368.

Branchiostegal counts on 4 specimens were 13-14, 14-14, 14-14, and 14-15. *Esox americanus* and *niger* were not taken together but both seem to prefer still or slow currents.

Stations: *22* (2, 65-80); *23* (1, 171); *38* (1, 91).

11. *Esox niger* LeSueur

Esox reticulatus.—Jordan, 1877a: 324; Jordan and Brayton, 1878: 48; Jordan, 1879: 104.

Esox niger.—Fowler, 1945: 351.

Stations: *39* (1, 320); *40* (1, 250).

HIODONTIDAE—Mooneyes

12. *Hiodon tergisus* LeSueur

Hyodon selenops.—Jordan and Brayton, 1878: 48 (Alabama River, Montgomery, Ala.).

Hiodon tergisus.—Scott, 1951: 37.

No new records.

CATOSTOMIDAE—Suckers

13. *Cycleptus elongatus* (LeSueur)

Cycleptus elongatus.—Scott, 1951: 38.

No new records.

14. *Ictiobus bubalus* (Rafinesque)

? Bubalichthys (taurus).—Jordan and Brayton, 1878: 55 ("Recorded by Professor Agassiz from the Alabama.").
Ictiobus bubalus.—Scott, 1951: 38.

Two specimens measuring 170 and 176 mm were collected at station *36*.

15. *Carpiodes cyprinus* (LeSueur)
Carpiodes cyprinus.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 55 (Montgomery, Ala.).

No recent records.

16. *Moxostoma duquesnei* (LeSueur)
? Moxostoma duquesnii var. *duquesnii* (in part).—Jordan, 1877a: 349.
Moxostoma duquesnii.—Hubbs, 1930: 19 (Alabama River drainage of Georgia; description).

Jordan (1878) abandoned *duquesnei* as a distinct species and regarded the character of 10 pelvic rays as an individual character and not a specific one. Jordan's opinion was followed until Hubbs (1930) studied the group and recommended that LeSueur's *Catostomus duquesnii* be recognized and known as *Moxostoma duquesnii* (LeSueur). Hubbs did not rely entirely on the pelvic ray count to distinguish *duquesnei* and found that about two-thirds of *duquesnei* had 10 pelvic rays.

A series of suckers collected in the Coosa River drainage of Alabama are tentatively assigned to *M. duquesnei.* They are easily distinguished from *M. erythrurum* and have all the characters of *duquesnei* except for the pelvic ray count. Eleven specimens measuring from 92 to 215 mm standard length all had no more than 9 pelvic rays. Two specimens had the pelvic fin formula of 8-9.

Stations: 8 (1, 104); *15* (1, 110); *16* (6, 193-270); *20* (1, 67); *23* (2, 84-253); *30* (1, 129); *32* (31, 23-35); *33* (6, 96-110, and 1, 228); *35* (1, 114); *46* (1, 162).

17. *Moxostoma erythrurum* (Rafinesque)
Myxostoma euryops Jordan, 1877a: 348, (original description; Oostanaula River, Ga.); Jordan and Brayton, 1878: 54; Jordan, 1879: 115.
Myxostoma macrolepidotum duquesnii.—Jordan and Brayton, 1878: 54.
Myxostoma macrolepidotum var. *dequesnei.*—Jordan, 1878: 120.
? Moxostoma macrolepidotum duquesnei.—Gilbert, 1891: 153.
Moxostoma erythrurum.—Fowler, 1945: 337.

M. erythrurum was never collected with *duquesnei. M. duquesnei* was found at elevations between 500 and 900 feet, whereas *erythrurum* was found at elevations between 400 and 500 feet.

Stations: 14 (1, 243); *22* (1, 64); *39* (3, 220-310); *44* (2, 32-102); *49* (1, 142).

18. *Moxostoma poecilurum* (Jordan)
Moxostoma poecilurum.—Gilbert, 1891: 153 (Attalla, Ala.); Hubbs, 1930: 30 (Alabama River, Benton, Ala.; key); Scott, 1951: 31.

Unlike *M. duquesnei* and *erythrurum, poecilurum* seems to prefer slower streams. One of 3 collections was made in the river. All of

the fins of *poecilurum* are bright red. It is quickly distinguished from the other suckers by the presence of the black bar through the lower caudal lobe. Dusky lateral stripes are in each scale row on the back and sides.

Stations: 33 (1, 225); *36* (1, 220); *53* (1, 111).

19. *Minytrema melanops* (Rafinesque)

Erimyzon melanops.—Jordan, 1877a: 347.

Minytrema melanops.—Jordan and Brayton, 1878: 54 (waters of the Alabama); Jordan, 1879: 115; Gilbert, 1891: 154 (Oxford, Ala.); Fowler, 1945: 338; Scott, 1951: 37.

No spots on scales below axis through upper part of mouth; venter very light in color.

Stations: 26 (2, 215-320); *39* (1, 240).

20. *Erimyzon sucetta* (Lacépède)

Erimyzon sucetta.—Jordan and Brayton, 1878: 54 (Alabama Basin); Jordan, 1878: 144 (description; nomenclature); 1879: 114; Gilbert, 1891: 153 (Calera, Ala.).

Jordan and Brayton (1878) gave no locality data other than "Alabama Basin." Possibly their specimens are from the lower Alabama System near Mobile. According to Hubbs (1930), Jordan (1878) confounded *sucetta* with *oblongus*. No recent records.

21. *Erimyzon oblongus* (Mitchill)

Erimyzon oblongus.—Jordan, 1877a: 346.

No recent records from the Coosa drainage; however, this sucker is known presently from other parts of the Mobile basin.

22. *Hypentelium etowanum* (Jordan)

Catostomus nigricans var. *etowanus* Jordan, 1877a: 345 (original description; Etowah River, Ga.); 1879: 114.

Catostomus nigricans etowanus.—Jordan and Brayton, 1878: 54 (Alabama Basin; Jordan, 1878: 162.

Hypentelium etowanum.—Jordan and Brayton, 1878: 86 (listed, Alabama Basin); Hubbs, 1930: 41 (description).

? Catostomus nigricans.—Gilbert, 1891: 153 (Alabama Basin).

Hypentelium nigricans etowanum.—Fowler, 1945: 339.

Collected from 20 stations at elevations from 200 to 900 feet, but mostly in clear, fast running streams above 500 feet. Only 5 of 63 specimens were taken below 500 feet.

Stations: 5 (2, 70-72, and 2, 126-142); *7* (3, 37-53, and 1, 230); *9* (3, 25-27; 6, 72-86 and 8, 98-152); *10* (1, 191); *11* (1, 130); *16* (2, 80-189); *20* (1, 80); *23* (6, 19-23); *24* (1, 65); *30* (2, 22-26); *31* (3, 27-32, and 1, 75); *32* (2, 34-35); *33* (2, 175-185); *34* (1, 30, and 5, 63-96); *35* (2, 30-32); *38* (1, 75); *41* (2, 26-96); *47* (1, 80); *50* (1, 64); *53* (2, 116-123).

CYPRINIDAE—Minnows

23. *Notemigonus crysoleucas* (Mitchill)

Notemigonus americanus.—Jordan, 1877a: 344.

Notemigonus chrysoleucus.—Jordan and Brayton, 1878: 53 (Alabama Basin); Jordan, 1879: 114; Gilbert, 1891: 155 (Calera, Ala.)

Stations: 37 (7, 26-37) and *53* (1, 58).

24. *Semotilus atromaculatus* (Mitchill)

Semotilus atromaculatus.—Gilbert, 1891: 155 (Alabama Basin).

Semotilus atromaculatus thoreauianus.—Fowler, 1945: 340.

Found most abundantly in clear, fast flowing streams above 1000 feet elevation. Only 3 collections were made below 700 feet, and none was below 450 feet.

Stations: *2* (62, 25-60); *5* (4, 61-73); 7 (5, 35-54); *9* (1, 60); *23* (11, 18-28); *27* (5, 50-84); *28* (3, 73-116); *30* (1, 50); *32* (3, 20-43); *35* (6, 40-71); *37* (3, 36-39).

25. *Hybopsis amblops* Rafinesque

Nocomis amblops var. *winchelli* Jordan, 1877a: 328.

Hybopsis gracilis.—Jordan, 1877a: 333.

Ceratichthys winchelli.—Jordan and Brayton, 1878: 53 ("common in the Alabama Basin").

Ceratichthys gracilis.—Jordan, 1879: 108.

Hybopsis amblops rubrifrons.—Gilbert, 1891: 155 (Attalla and Oxford, Ala.).

? Erinemus hyalinus.—Fowler, 1945: 341 (color description).

This species seems to have a preference for slow moving streams.

Stations: 31 (6, 50-56); *34* (2, 51); *36* (44, 58-116); *48* (1, 60).

26. *Rhinichthys atratulus* (Hermann)

Rhinichthys obtusus.—Jordan, 1877a: 331; Jordan and Brayton, 1878: 54; Jordan, 1879: 109.

Rhinichthys atronasus obtusus.—Jordan, 1877a: 369.

Rhinichthys atronasus croceus.—Fowler, 1945: 342.

No new records.

27. *Phenacobius catostomus* Jordan

Phenacobius catostomus Jordan, 1877a: 332 (original description; Silver Creek, Etowah River, Ga.).—Jordan and Brayton, 1878: 53; Jordan, 1879: 109.

Not common anywhere in the Coosa drainage of Alabama.

Stations: 6 (1, 66); *14* (2, 75-80); *31* (1, 63); *33* (3, 70-83).

28. *Notropis volucellus* (Cope)

Notropis volucellus.—Howell, 1957: 56 (Little Canoe Creek, St. Clair-Etowah County line).

This species, distinguished from other *Notropis* of the Coosa drainage by the high, narrow, anterior lateral line scales, was first reported in these waters by Howell (1957).

Stations: 14 (2, 38-40); *19* (4, 50-61); *20* (1, 50); *23* (2, 52-60).

29. *Notropis venustus stigmaturus* (Jordan)

Photogenis stigmaturus Jordan, 1877a: 337 (original description; Etowah, Oostanaula and Coosa Rivers, Ga.).

Codoma stigmaturus.—Jordan and Brayton, 1878: 50.

Codoma stigmatura.—Jordan, 1879: 111.

Notropis venustus cerostigma.—Gilbert, 1891: 154 (Alabama Basin).

Notropis stigmaturus.—Fowler, 1910: 281 (Etowah R.); 1923; 20 (Rome, Ga.); 1945: 344.

Erogala stigmatura.—Fowler, 1935: 72 (Armuchee, Ga.).

Notropis venustus stigmaturus.—Gibbs, 1957: 192 (upper Alabama River; description; distribution).

This minnow was found abundantly throughout the study area.

Breeding males and gravid females were common at those stations where series were taken.

Lateral line scale counts and depth measurements of 113 specimens varied from 39 to 46 and from 18.4 to 24.5 per cent of standard length respectively. The body depth figures exceed the upper limits of 22.5 per cent of standard length given by Gibbs (1957) for *Notropis venustus stigmaturus;* however, gravid females were among the lot measured.

The following measurements are in standard lengths and to the nearest millimeter.

Stations: 15 (2, 56-64); *17* (4, 53-84); *20* (6, 49-57); *22* (20, 51-95); *23* (3, 31-54); *29* (1, 96); *30* (3, 54-77); *31* (67, 48-69); *32* (18, 32-42); *35* (1, 76); *37* (2, 60-61); *38* (3, 30-53); *44* (18, 42-78); *46* (6, 51-98); *47* (8, 47-88); *48* (1, 69); *53* (25, 47-84).

30. *Notropis callistius* (Jordan)

Photogenis callistius Jordan, 1877a: 337 (original description; Etowah and Oostanaula Rivers, Ga.)

Codoma callistius.—Jordan and Brayton, 1878: 50.

Codoma callistia.—Jordan, 1879: 111.

Notropis callistius.—Gilbert, 1891: 154 (Alabama Basin); Fowler, 1910: 281 (Etowah R.), 1945: 344; Howell, 1957: 93 (Terrapin Creek, Piedmont, Calhoun Co., Ala.).

Breeding males with well developed tubercles were observed at several stations.

Stations: 11 (1); *17* (1, 85); *20* (2, 37-40, and 1, 85); *29* (4, 44-67); *30* (2, 37-45); *46* (2, 60-65); *47* (9, 55-94).

31. *Notropis trichroistius* (Jordan and Gilbert)

Codoma trichroistia Jordan and Gilbert *in* Jordan and Brayton, 1878: 50 (original description; Etowah R., Rome, Ga.).—Jordan, 1879: 111.

Notropis trichroistius.—Gilbert, 1891: 154 (Alabama Basin); Fowler, 1945: 344; Howell, 1957: 102 (Little Canoe Cr.).

The tricolor shiner prefers clear, cool streams and was not collected at elevations of less than 500 feet. Breeding males were collected. The tubercles are prominent but smaller than those of *N. callistius.* The body is light steel blue above, becoming silvery below. The subcaudal spot is deep blue. The pectoral, pelvic, and caudal fins are pink. Jet black patches are found between the posterior dorsal rays. The tip of the dorsal fin is bright red and the base is deep blue-black. The tips of the anal, pelvic and pectoral fins are also bright red.

Stations: 1 (17, 35-71); *9* (36, 42-80); *16* (2, 40-56); *19* (2, 36-48); *20* (32, 27-62); *24* (4, 26-32, and 7, 40-67); *27* (1, 69); *29* (2, 27-30, and 20, 41-98); *30* (16, 36-74); *31* (21, 42-67); *34* (16, 43-73); *35* (18, 30-44, and 25, 51-76); *38* (86, 25-74).

32. *Notropis caeruleus* (Jordan)

Photogenis caeruleus Jordan, 1877a: 338 (original description; tributaries of the Oostanaula River, above Rome, Ga.).

Erogala caerulea.—Jordan and Brayton, 1878: 51 (Oostanaula River and its tributaries).
Codoma caerulea.—Jordan, 1879: 111.
Notropis coeruleus.—Gilbert, 1891: 154 (Attalla and Oxford, Ala.).
Notropis caeruleus.—Fowler, 1910: 282; 1945: 345.

This minnow, endemic to the Alabama Basin, is not common anywhere within its range. The scales of the back and sides are marked much like those of *Notropis venustus*. The ground color of the back and sides of specimens fresh from the water is light olive blue, and the lateral band is rich steel blue. The posterior end of the lateral band is only slightly expanded and little darker. The fins are light pink with few melanophores. The belly is silvery. The snout is blunter and the body deeper than other members of the subgenus *Cyprinella* listed herein.

Three specimens measuring from 50 to 80 mm were collected at station *23*.

33. *Notropis asperifrons* Suttkus and Raney
Notropis asperifrons Suttkus and Raney, 1955b: 3-33 (original description; Holly Creek, Murray Co., Ga.; paratypes from the Coosa River drainage are from Cherokee, Calhoun, Talladega, and Shelby Counties, Ala., and Whitfield Co., Ga.).
Stations: 16 (1, 61); *19* (3, 50-62); *20* (2, 51-64); *22* (1, 58); *29* (24, 39-67); *31* (6, 36-55); *38* (27, 40-59); *39* (18, 38-53); *40* (2, 50-51); *44* (1, 50).

34. *Notropis baileyi* Suttkus and Raney
Notropis baileyi Suttkus and Raney, 1955a: 71-86 (original description; Sawacklahatchee Creek, Macon Co., Ala.).

Suttkus and Raney (1955a) reported a single specimen of *N. baileyi* in the Coosa River System from Etowah Co., Ala. This remains the northernmost record for the species. Fifty-five specimens collected from 5 stations in the southernmost 3 counties of the study area further verifies the presence of the species in the Coosa drainage.
Stations: 46 (17, 46-68); *47* (13, 51-60); *48* (11, 51-73); *50* (13, 30-56); *52* (1, 57).

35. *Notropis xaenocephalus* (Jordan)
Hybopsis xaenocephalus Jordan, 1877a: 334 (original description; Etowah, Oostanaula and Coosa Rivers, Ga.).
Hydrophlox xaenocephalus.—Jordan and Brayton, 1878: 49.
Alburnops xaenocephalus.—Jordan, 1879: 110.
Notropis xaenocephalus.—Gilbert, 1891: 154 (Alabama Basin); Fowler, 1910: 288 (Etowah R.), 1945: 346; Howell, 1957: 162 (St. Clair and Etowah Co.).

Generally distributed throughout the Coosa drainage of Alabama, and often associated with *N. chrosomus* but rarely with *N. asperifrons*.
Stations: 7 (9, 22-47); *9* (18, 45-68); *13* (9, 21-47); *14* (6, 23-49); *23* (4, 41-46); *24* (21, 32-56); *26* (5, 50-67); *30* (33, 44-66); *34* (15, 43-64); *35* (26, 47-64); *41* (5, 53-57); *44* (1, 40).

36. *Notropis chrosomus* (Jordan)
Hybopsis chrosomus Jordan, 1877a: 333 (original description; Etowah River, Ga.).

Hydrophlox chrosomus.—Jordan and Brayton, 1878: 49.
Alburnops chrosomus.—Jordan, 1879: 110.
Notropis chrosomus.—Fowler, 1910: 287 (Etowah R.), 1945: 346; Howell, 1957: 181 (Etowah Co., Ala.).

The body of live specimens is multicolored with an iridescence of blues and reds. The almost undiscernible longitudinal alternating light and dark bands along the back and sides are obscured by the iridescence. The bases of the dorsal, anal, and pelvic fins are red. The pectoral fins are pink; the caudal fin has scattered melanophores in the central portion.

Stations: 5 (14, 44-66); *7* (12, 43-57); *16* (8, 51-64); *22* (1, 46); *24* (10, 34-60); *31* (1, 57); *34* (4, 57-70); *35* (5, 46-55); *38* (17, 46-58); *41* (1, 63); *44* (2, 46-57).

37. *Notropis cornutus* (Mitchill)

Luxilus cornutus.—Jordan, 1877a: 340; Jordan and Brayton, 1878: 49; Jordan, 1879: 110.
Notropis megalops.—Gilbert, 1891: 154 (Alabama Basin).
Notropis cornutus chrysocephalus.—Fowler, 1945: 345.
Notropis cornutus.—Howell, 1957: 193.

Especially abundant in the lower 2/3 of the Coosa drainage of Alabama.

Stations: 7 (11); *14* (2); *16* (3, 67-80, and 1, 118); *18* (1, 70); *19* (2, 33-70); *23* (1, 56); *26* (1, 103); *31* (11, 70-157); *32* (2, 82-91); *33* (2, 77-80); *34* (7, 77-123); *38* (3, 56-57); *39* (3, 63-75) *44* (1, 133); *47* (4, 64-69); *48* (14, 57-78); *50* (4, 59-71); *53* (27, 47-80).

38. *Notropis atherinoides* Rafinesque

Notropis atherinoides was reported in the Coosa River for the first time by Howell (1957). It is very similar to *N. stilbius* but may be distinguished from it by the character of the slightly more slender and compressed body and by the shorter snout. Howell pointed to the fact that *atherinoides* prefers larger streams. This observation also applied to specimens from the Coosa drainage. Of the three collections, two were made in the river proper and one in a sluggish stream only one mile from the river.

Stations: 36 (200, 30-57); *37* (5, 52-64); *51* (1, 59).

39. *Notropis stilbius* (Jordan)

Nototropis stilbius Jordan, 1877a: 343 (original description; Etowah River, Ga.).
Notropis stilbius.—Jordan and Brayton, 1878: 53 (Alabama Basin); Jordan, 1879: 111; Gilbert, 1891: 154 (Alabama Basin); Fowler, 1910: 289 (Etowah R.), 1935: 72 (Armuchee, Ga.), 1945: 349; Howell, 1957: 225 (Little Canoe Cr.).

Unlike *N. atherinoides*, *stilbius* is found in smaller streams usually at considerable distances from the river. It was collected at elevations from 400 to 600 feet.

Stations: 14 (18, 36-64); *19* (3, 52-53); *22* (16, 55-76); *31* (25, 42-69); *32* (1, 69); *33* (1, 58); *34* (1, 64); *44* (1, 73); *46* (3, 64-74); *47* (1, 58); *49* (15, 42-69).

40. *Notropis bellus* (Hay)

Breeding males and females were collected at both stations. This apparently represents the first record of the species in the Coosa River system.

Stations: *44* (10, 48-62); *52* (21, 53-69).

41. *Notropis lirus* (Jordan)

Nototropis lirus Jordan, 1877a: 342 (original description; Etowah R., Ga.).

Notropis lirus.—Jordan and Brayton, 1878: 53; Jordan, 1879: 113; Fowler, 1945: 238 (Etowah R.), 348.

Males with well developed tubercles and gravid females were collected at several stations. The smallest gravid female was 42 mm total length.

Stations: *16* (2 of 15, 47-49); *18* (6, 38-54); *19* (3, 46-52); *20* (15, 38-54); *26* (1 of 10, 55); *30* (1, 55); *31* (3 of 10, 37-55); *34* (3, 36-41); *35* (1 of 8, 53); *38* (19 of 85, 27-52); *39* (1 of 15, 40); *40* (18, 42-54).

42. *Ericymba buccata* Cope

This distinctive minnow, not previously reported from the Coosa System, was taken in 2 collections over rock, sand and gravel.

Stations: *53* (9, 35-60); *54* (2, 25-26, and 6, 41-60).

43. *Pimephales vigilax* (Baird and Girard)

Cliola vigilax.—Gilbert, 1891: 154 (Attalla, Ala.).

Lythrurus lirus.—Fowler, 1935: 72 (Armuchee, Ga.; corrected by Fowler (1945: 233) to *Certalichthys vigilax*).

Ceratichthys velox.—Fowler, 1945: 342.

No new records.

44. *Pimephales notatus* (Rafinesque)

Hyborhynchus notatus.—Fowler, 1945: 340.

No new records.

45. *Campostoma anomalum* (Rafinesque)

Campostoma anomalum var. *anomalum* Jordan, 1877a: 325.

Campostoma anomalum var. *prolixum* Jordan and Brayton, 1878: 49.

Campostoma anomalum.—Jordan, 1879: 107; Gilbert, 1891: 154 (Alabama Basin); Fowler, 1935: 72 (Armuchee, Ga.).

Campostoma anomalum anomalum.—Fowler, 1945: 340.

Very abundant throughout the Coosa drainage of Alabama.

Stations: *7* (5, 32-52); *9* (5, 63-82); *14* (2, 34-82); *16* (1, 41); *19* (5, 26-31); *20* (1, 101); *22* (1, 118); *24* (2, 48-67); *25* (1, 110); *26* (1, 36); *31* (3, 29-30, and 2, 57-67); *32* (3, 26-32, and 2, 85); *33* (2, 77-80); *34* (2, 29-55); *35* (9, 20-38, and 5, 61-73); *37* (1, 35); *38* (2, 71-94); *41* (8, 18-38, and 1, 60); *53* (1, 61).

ICTALURIDAE—Catfishes

46. *Ictalurus punctatus* (Rafinesque)

Ichthaelurus punctatus.—Jordan, 1877a: 350; Jordan and Brayton, 1878: 55 (basin of the Alabama).

Ictalurus punctatus.—Gilbert, 1891: 153 (Attalla, Ala.); Fowler, 1935: 72 (Armuchee, Ga.).

Ictalurus lacustris punctatus.—Fowler, 1945: 350; Scott, 1951: 31.

Taken only in the river proper.

Stations: *36* (67, 40-90, and 1, 137); *43* (12, 192-230); *51* (2, 160).

47. *Ictalurus furcatus* (LeSueur)

? Ictalurus ponderosus.—Fowler, 1945: 350 (identification from photograph).

Ictalurus furcatus.—Scott, 1951: 31.

Six specimens measuring from 190 to 230 mm were taken in traps at station *43*.

48. *Ictalurus natalis* (LeSueur)

Amiurus cupreus.—Jordan, 1877a: 351.

Amiurus lividus.—Jordan, 1877a: 368.

Amiurus natalis antoniensis.—Jordan and Brayton, 1878: 55.

Ameiurus natalis erebennus.—Fowler, 1945: 350.

No new records.

49. *Ictalurus melas* (Rafinesque)

Ameiurus melas melas.—Fowler, 1945: 350.

One specimen measuring 66 mm was collected at station *35*.

50. *Pylodictis olivaris* (Rafinesque)

Pilodictis olivaris.—Scott, 1951: 31.

One specimen measuring 232 mm was collected at station *36*.

51. *Noturus leptacanthus* Jordan

Noturus leptacanthus Jordan, 1877a: 352 (original description; Etowah River, Rome, Ga.).—Jordan and Brayton, 1878: 55; Jordan, 1879: 119; Gilbert, 1891: 153 (Attalla, Ala.).

Schilbeodes leptacanthus.—Fowler, 1945: 351; Scott, 1951: 37.

No new records.

ANGUILLIDAE—Freshwater Eels

52. *Anguilla rostrata* (LeSueur)

Anguilla vulgaris.—Jordan, 1877a: 352; Jordan and Brayton, 1878: 55 (Alabama Basin); Jordan, 1879: 119.

One specimen measuring 315 mm was collected at station *51*.

AMBLYOPSIDAE—Cave Fishes

53. *Typhlichthys subterraneus* Girard

A series of 10 specimens collected at station *4* is tentatively assigned to this species. This constitutes the first record of the genus in the Mobile basin.

CYPRINODONTIDAE—Topminnows

54. *Fundulus stellifer* (Jordan)

Xenisma stellifer Jordan, 1877a: 322 (original description; Etowah, Oostanaula and Coosa Rivers, near Rome, Ga.).

Xenisma stelliferum.—Jordan and Brayton, 1878: 48; Jordan, 1879: 103.

Fundulus stellifer.—Gilbert, 1891: 155 (Attalla and Oxford, Ala.); Fowler, 1945: 352.

This minnow, endemic to the Coosa River system of Alabama and Georgia, is one of the most colorful of freshwater cyprinodont

fishes. Adult males, fresh from the water, have an iridescence dominated by greenish-blue. Bright red specks are present over most of the body, head, dorsal fin, and base of anal fin. The red specks usually form irregularly broken lateral stripes. The dorsal, caudal, anal, and pelvic fins are pale pinkish; the pectorals are practically clear. Most striking in adult males is the jet black band bordering the dorsal and caudal fins.

The females and young males are less colorful. The ground color is light olive; the fins are very pale, except for the dorsal and caudal which are light straw color. Most of the head and body are covered with olive-black specks. The belly is silvery.

Females with mature eggs were observed at several stations.

Stations: 7 (8, 50-67); *16* (1, 51, and 5, 88-105); *23* (1, 91); *24* (7, 47-83); *30* (1, 37, and 2, 85-95); *31* (15, 45-96); *35* (4, 60-81).

55. *Fundulus notatus* (Rafinesque)

Fundulus notatus.—Fowler, 1945: 352.

Brown (1956) listed *Fundulus olivaceus* from the Alabama River and *F. notatus* from the Tombigbee River, Alabama. Our Coosa River specimens are tentatively assigned to *F. notatus* until an analysis of the Mobile basin *notatus-olivaceus* complex is completed. The modal number of dorsal and anal rays is 10 and 12, respectively. The mean is 9.6 and 11.8, respectively. We recognize sexual dimorphism, as well as a high degree of color pattern variation within sexes. Several females were heavy with mature eggs.

Stations: 15 (2, 52-60); *16* (4, 45-61); *18* (2, 50-64); *22* (2, 60-63); *31* (13, 40-67); *40* (1, 69); *42* (2, 58-61); *44* (2, 51-58); *51* (1, 62); *52* (5, 51-72); *53* (3, 45-64).

56. *Gambusia affinis* (Baird and Girard)

Gambusia patruelis.—Fowler, 1945: 352.

The ratio of males to females was 1: 6. Many of the females were heavy with young.

Stations: 12 (4 females, 32-50); *18* (1 female, 37); *19* (7 females, 35-49); *23* (27 females, 15-45, and 8 males, 22-28); *26* (18 females, 19-51, and 2 males, 30-31; *29* (2 females, 40); *37* (5 females, 37-43, and 1 male, 23); *38* (1 female, 40).

APHREDODERIDAE—Pirate Perches

57. *Aphredoderus sayanus* (Gilliams)

Aphododerus sayanus.—Jordan, 1877a: 368 (listed; Coosa R.); Jordan and Brayton, 1878: 47 (Alabama River, Montgomery, Ala.).

No recent records.

MUGILIDAE—Mullets

58. *Mugil cephalus* Linnaeus

Mugil cephalus.—Byrd, 1954: 3 (Coosa River near Wetumpka, Ala.); Boschung and Hemphill, 1960: 73 (distribution in fresh water).

Two specimens measuring approximately 250 mm were found dead on the beach at station *51*. Striped Mullet have been observed in the Cahaba and Coosa Rivers in Alabama for several years. They are caught on hook and line using earthworms for bait.

SERRANIDAE—Basses

59. *Roccus saxatilis* (Walbaum)

Roccus striatus.—Bean, 1884: 242 (Montgomery, Ala.).

Concerning *Roccus saxatilis*, I. B. Byrd, Chief Biologist, Fisheries Section, Alabama Department of Conservation, stated, "Peak runs of saltwater striped bass up the Coosa to Jordan Dam and up the Tallapoosa to Tallassee Dam occur each year during May and June. Hundreds of fishermen fish below these two dams — particularly below the Tallassee Dam for the stripes. Specimens of 10 to 25 pounds are commonly caught. One 55-pounder was taken last year below Tallassee Dam."

60. *Roccus chrysops* (Rafinesque)

Lepibema chrysops.—Scott, 1951: 31.

Two specimens measuring 130 and 140 mm were collected at station *36*.

CENTRARCHIDAE—Sunfishes

61. *Micropterus punctulatus henshalli* Hubbs and Bailey

Micropterus punctulatus henshalli.—Fowler, 1945: 361; Scott, 1951: 31.

Micropterus pallidus (in part).—Jordan, 1877a: 314; Jordan and Brayton, 1878: 46; Jordan, 1879: 100.

Micropterus pseudaplites (in part).—Hubbs, 1927: 13 (Rome, Ga.).

Stations: 14 (2, 40-106); *22* (2, 84-98); *45* (2, 49-108); *51* (1, 43).

62. *Micropterus coosae* Hubbs and Bailey

Micropterus coosae Hubbs and Bailey, 1940: 23 (original description; Big Will's Creek, Etowah Co., Ala.).—Fowler, 1945: 361.

Micropterus salmoides (in part).—Jordan, 1877a: 314.

Micropterus salmoides var. *salmoides*.—Jordan and Brayton, 1878: 46 (Alabama Basin).

Micropterus pseudaplites (in part.—Hubbs, 1927: 13 (Rome, Ga.).

Stations: 3 (1, 136); *5* (1, 88); *9* (2, 74-84); *24* (1, 59); *37* (1, 113); *39* (1, 241); *53* (1, 108).

63. *Micropterus salmoides* (Lacépède)

Micropterus salmoides (in part).—Jordan, 1877a: 314; Jordan and Brayton, 1878: 46 (Alabama Basin); Jordan, 1879: 100; Gilbert, 1891: 155 (Alabama Basin).

Micropterus pallidus (in part).—Jordan, 1877a: 314.

M. salmoides, the largemouth black bass, seems to be more common in the Coosa River drainage of Alabama than the preceeding two species of the genus *Micropterus*.

Stations: 23 (3, 26-40; 1, 97, and 1, 310); *28* (2, 98-100); *31* (1, 37); *32* (4, 22-59); *36* (3, 135-197); *37* (1, 152); *42* (4, 43-48); *44* (1, 166); *52* (1, 51); *53* (2, 58-143).

64. *Chaenobryttus gulosus* (Cuvier)

Chaenobryttus gulosus.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 46 (Alabama River, Montgomery, Ala.).

Chaenobryttus coronarius.—Scott, 1951: 31.

Stations: 9 (1, 115); *23* (1, 140); *39* (1, 110).

65. *Lepomis cyanellus* Rafinesque

Lepomis cyanellus.—Scott, 1951: 31.

Stations: 27 (14, 53-108); *28* (1, 65); *29* (1, 36); *35* (2, 60-68); *54* (4, 66-80).

66. *Lepomis microlophus* (Gunther)

Twelve specimens from 5 stations are referable to this species. These constitute what are apparently the first records of the species from the Coosa River System.

Stations: 15 (1, 125); *18* (3, 63-74); *29* (5, 43-74); *42* (2, 72-125); *51* (1, 142).

67. *Lepomis megalotis* (Rafinesque)

Xenotis sanguinolentus.—Jordan, 1877a: 318; Jordan and Brayton, 1878: 46; Jordan, 1879: 98.

Xenotis inscriptus.—Jordan, 1877a: 318, 1877b: 42 (Etowah R.); Jordan and Brayton, 1878: 46.

Lepomis megalotis megalotis.—Gilbert, 1891: 155 (Alabama Basin); Fowler, 1945: 360; Scott, 1951: 31.

Abundant throughout the area.

Stations: 2 (4, 40-55); *8* (1, 103); *13* (5, 66-92); *14* (3, 37-71); *18* (1, 66); *19* (1, 38); *22* (3, 44-45); *31* (5, 45-95); *32* (2, 62-70); *33* (2, 122-129); *37* (2, 67-75); *39* (4, 33-51); *40* (3, 33-41); *44* (1, 64); *45* (1, 38); *52* (4, 60-90); *53* (4, 41-73).

68. *Lepomis macrochirus* Rafinesque

Lepiopomus obscurus.—Jordan, 1877a: 317 (description); Jordan and Brayton, 1878: 46; Jordan, 1879: 99.

Lepiopomus pallidus.—Jordan, 1877a: 316; Jordan and Brayton, 1878: 46; Jordan, 1879: 99.

Helioperca obscura.—1877a: 369 (listed).

? Helioperca pallida.—Jordan, 1877a: 369 (listed).

? Eupomotis pallidus.—Jordan, 1877a: 368 (listed); 1877b: 21 (Alabama River).

Lepomis macrochira macrochira.—Fowler, 1945: 360.

Lepomis macrochirus macrochirus.—Scott, 1951: 31.

Abundant throughout the area.

Stations: 8 (2, 50-77); *13* (1, 85); *14* (7, 42-104); *15* (2, 56-78); *16* (3, 45-50); *17* (1, 35); *18* (2, 41-60); *19* (2, 40-75); *20* (1, 65); *22* (7, 45-72); *28* (1, 44); *29* (4, 30-55); *30* (13, 28-46); *31* (14, 29-37, and 1, 161); *33* (1, 165); *37* (3, 24-27, and 1, 65); *39* (1, 52); *41* (1, 58); *42* (4, 47-98); *49* (1, 67); *51* (2, 72-85); *53* (6, 37-48).

69. *Ambloplites rupestris* (Rafinesque)
Ambloplites rupestris.—Jordan, 1877a: 316; Jordan and Brayton, 1878: 46; Jordan, 1879: 100.
Ambloplites rupestris rupestris.—Scott, 1951: 37.
No new records.

70. *Pomoxis nigromaculatus* (LeSueur)
Pomoxys hexacanthus.—Jordan, 1877a: 368.
One specimen measuring 111 mm was collected at station *23*.

71. *Pomoxis annularis* Rafinesque
Pomoxys annularis.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 47 (Round Lake, Montgomery, Ala.).
Pomoxis annularis.—Scott, 1951: 31.
One specimen measuring 95 mm was collected at station *18*.

72. *Centrarchus macropterus* (Lacépède)
Centrarchus irideus.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 47 (Alabama River, Montgomery, Ala.).
No recent records. This species is known presently from the Warrior River drainage of the Mobile basin.

PERCIDAE—Perches

73. *Stizostedion vitreum* (Mitchill)
Stizostethium salmoneum.—Jordan, 1877a: 313; Jordan and Brayton, 1878: 45; Jordan, 1879: 96.
Stizostedion vitreum vitreum.—Fowler, 1945: 352; Scott, 1951: 37.
No new records.

74. *Percina caprodes* (Rafinesque)
Percina caprodes.—Jordan, 1877a: 312; Jordan and Brayton, 1878: 45 (Alabama River).
Etheostoma caprodes.—Gilbert, 1891: 155 (Alabama Basin).
Percina caprodes caprodes.—Fowler, 1945: 354.
Stations: 6 (3, 112-116); *21* (1, 85); *33* (1, 90); *38* (4, 70-102); *39* (1, 99); *40* (1, 107); *42* (5, 48-97); *44* (1, 123); *47* (1, 105); *49* (2, 95-107); *52* (1, 90).

75. *Percina nigrofasciata* (Agassiz)
Hadropterus nigrofasciatus.—Jordan, 1877a: 310; Jordan and Brayton, 1878; 45 (Alabama Basin); Jordan, 1879: 96.
Etheostoma nigrofasciatum.—Gilbert, 1891: 155 (Alabama Basin).
Hadropterus nigrofasciatus nigrofasciatus.—Fowler, 1945: 354.
Percina nigrofasciata nigrofasciata.—Crawford, 1956: 8 (records from the Coosa River drainage of Alabama and Georgia; description).
Stations: 9 (5, 63-82); *22* (3, 43-70); *26* (9, 47-93); *38* (1, 61).

76. *Percina palmaris* (Bailey)
Hadropterus palmaris Bailey, 1940: 524-580 (original description; Etowah River, Lumpkin Co., Ga.).—Crawford, 1954: 235 (tributaries of the Etowah River, Ga., and Cherokee-Calhoun Co. line, Ala.).
Crawford (1954) listed a collection "Cornell University . . . No. 21158, Cherokee-Calhoun Co. line on Rte. 74, Ga." Undoubtedly Crawford intended to list the record from Alabama. Cherokee County, Alabama is adjacent to Calhoun County, and Route 74 is an Alabama State highway and also U.S. highway 278.
One specimen measuring 67 mm was collected at station *48*.

77. *Ammocrypta asprella* (Jordan)
Pleurolepis asprellus.—Jordan and Brayton, 1878: 82 (Montgomery, Ala.).
Etheostoma asprellum.—Gilbert, 1891: 155 (Oxford, Ala.).
No recent records.

78. *Etheostoma stigmaeum* (Jordan)
Boleosoma stigmaeum Jordan, 1877a: 307 (original description; Etowah and Oostanaula Rivers, Ga.).
Ulocentra stigmaea.—Jordan and Brayton, 1878: 45 (Alabama Basin); Fowler, 1945: 354.
Etheostoma stigmaeum.—Gilbert, 1891: 155 (Alabama Basin).
Stations: 6 (1, 48); *7* (1, 48); *9* (1, 54); *31* (3, 40-43); *34* (5, 35-46); *35* (3, 45-53); *37* (3, 51-53); *38* (1, 43).

79. *Etheostoma blennioides* Rafinesque
Etheostoma blennioides.—Fowler, 1945: 355.
No new records.

80. *Etheostoma coosae* (Fowler)
Poecilichthys coosae Fowler, 1945: 356 (original description; Coosa River, Cherokee Co., Ala.).
Etheostoma (Ulocentra) coosae.—Bailey and Gosline, 1955: 40 (listed, Floyd and Polk Co., Ga., and Etowah Co., Ala.).
No new records.

81. *Etheostoma (Ulocentra)* sp.
This undescribed species is represented by 34 specimens.
Stations: 5 (3); *7* (6); *9* (4); *13* (4); *14* (1); *16* (1); *24* (7); *35* (1); *38* (6); *44* (1).

82. *Etheostoma jordani* Gilbert
Etheostoma (Nothonotus) jordani Gilbert, 1891: 156 (original description; Choccolo Creek, Oxford, and Chestnut Creek, Verbena, Ala.).—Bailey and Gosline, 1955: 40 (listed, Whitfield Co., Ga.).
One specimen measuring 53 mm was collected at station *36*.

83. *Etheostoma whipplei; artesiae* (Hay)
Three specimens measuring from 44 to 49 mm were collected at station *40*. Although this species is known from the Warrior drainage, these specimens apparently constitute the first records of the species from the Coosa.

SCIAENIDAE—Drums

84. *Aplodinotus grunniens* Rafinesque
Haploidonotus grunniens.—Jordan, 1877a: 319; Jordan and Brayton, 1878: 47; Jordan, 1879: 101.
Aplodinotus grunniens.—Scott, 1951: 31.
Three specimens measuring from 81 to 90 mm were collected at station *36*.

COTTIDAE—Sculpins

85. *Cottus carolinae* (Gill)
Potamocottus zopherus Jordan, 1877a: 320 (original description; Etowah and Oostanaula Rivers, Ga.); 1879: 102.
Potamocottus meridionalis.—Jordan and Brayton, 1878: 47.

Cottus bairdi.—Gilbert, 1891: 157 (Attalla and Oxford, Ala.).
? Cottus bairdii bairdii.—Fowler, 1945: 362.
Stations: *6* (53, 22-68); *7* (1, 63); *22* (3, 23-25); *23* (1, 26); *26* (1, 28); *29* (1, 22); *35* (2, 25-55); *38* (2, 25-29); *41* (1, 32).

SPECIES OF DOUBTFUL OCCURRENCE

The following species have been reported from the Coosa River system by previous authors, but their occurrence there seems doubtful.

86. *Semotilus corporalis* (Mitchill)
Semotilus corporalis.—Jordan, 1877a: 327; Jordan and Brayton, 1878: 54; Jordan, 1879: 107.

87. *Notropis rubricroceus* (Cope)
Notropis rubricroceus.—Fowler, 1945: 345.

88. *Notropis photogenis* (Cope)
Notropis photogenis.—Fowler, 1945: 349.

89. *Etheostoma simoterum* (Cope)
Etheostoma simoterum.—Gilbert, 1891: 155 (Alabama Basin).

90. *Boleichthys elegans* Girard
Boleichthys elegans.—Jordan, 1877a: 308; Jordan and Brayton, 1878: 45 (Alabama Basin); Jordan, 1879: 94.

91. *Etheostoma squamiceps* Jordan
Etheostoma squamiceps.—Gilbert, 1891: 156 (Calera, Ala.).

DISTRIBUTION

Ten species (*Hypentelium etowanum, Notropis callistius N. trichroistius, N. caeruleus, N. xaenocephalus, N. chrosomus, Fundulus stellifer, Percina palmaris, Etheostoma coosae,* and *E. jordani*) and possibly the undescribed Etheostomid of the subgenus *Ulocentra* are endemic to the upper Alabama system. *Notropis asperifrons* and *N. venustus stigmaturus* of the Coosa fauna are limited to the Mobile basin. *Notropis baileyi, N. stilbius, N. bellus, Noturus leptacanthus,* and *Micropterus coosae* are Coosa fishes that are also found in two or more Gulf drainages east of the Mississippi. It is probable that they originated in the Mobile basin. *Phenacobius catostomus* and *Notropis lirus* are shared by the Coosa and Tennessee systems and probably originated in the latter.

Two (*Mugil cephalus* and *Roccus saxatilis*) are marine forms which migrate upstream to the base of Jordan Dam. The dam also serves as a barrier to further upstream migration of the euryhaline shad, *Alosa chrysochloris. Anguilla rostrata,* historically known from the Etowah and Oostanaula Rivers of Georgia (Jordan, 1877a), and *Ericymba buccata* were not collected in the Coosa above Jordan Dam. *Dorosoma petenense* is represented in the lakes by residual populations. In addition to these species, *Ictiobus bubalus, Notropis atherinoides, N. bellus, Pylodictis olivaris, Roccus chrysops,* and *Etheostoma whipplei artesiae* are not known in the Coosa drainage above station *36* (Fig. 1).

Excluding the 6 species of doubtful occurrence, the fish fauna of the Coosa River drainage of Georgia and Alabama comprise 20 families and 85 species. Ten (*Polyodon spathula, Alosa chrysochloris, Dorosoma pretenense, Notropis volucellus, N. atherinoides, N. bellus,*

Ericymba buccata, Typhlichthys subterraneus, Lepomis microlophus, and *Etheostoma whipplei artesiae*) are reported herein from the Coosa drainage for the first time.

CLASSIFICATION OF THE FISHES OF THE COOSA DRAINAGE OF ALABAMA BASED ON HABITAT PREFERENCES

I. Species limited to streams and tributaries.

Ichthyomyzon gagei
Esox americanus
Esox niger
Moxostoma erythrurum
Hypentelium etowanum
Notemigonus crysoleucas
Semotilus atromaculatus
Rhinichthys atratulus
Phenacobius catostomus
Notropis volucellus
Notropis venustus stigmaturus
Notropis callistius
Notropis trichroistius
Notropis caeruleus
Notropis asperifrons
Notropis baileyi
Notropis xaenocephalus
Notropis chrosomus
Notropis cornutus
Notropis stilbius
Notropis bellus
Notropis lirus
Ericymba buccata
Pimephales vigilax
Pimephales notatus
Campostoma anomalum
Ictalurus natalis[1]
Ictalurus melas[1]
Fundulus stellifer
Gambusia affinis
Micropterus coosae[1]
Chaenobryttus gulosus[1]
Pomoxis nigromaculatus[1]
Percina nigrofasciata
Percina palmaris
Ammocrypta asprella
Etheostoma stigmaeum
Etheostoma blennioides
Etheostoma coosae
Etheostoma (Ulocentra) sp.
Etheostoma whipplei artesiae
Cottus carolinae

II. Species limited to the river and the impounded waters.

Polyodon spathula
Acipenser fulvescens
Lepisosteus osseus
Alosa chrysochloris
Dorosoma cepedianum
Dorosoma petenense
Hiodon tergisus
Cycleptus elongatus
Ictiobus bubalus
Ictalurus punctatus
Ictalurus furcatus
Pylodictis olivaris
Anguilla rostrata
Mugil cephalus
Roccus saxatilis
Roccus chrysops
Aplodinotus grunniens

III. Species known to occur in both the river and the tributaries.

Moxostoma poecilurum
Minytrema melanops
Hybopsis amblops
Notropis atherinoides
Noturus leptacanthus
Fundulus notatus
Micropterus punctulatus henshalli
Micropterus salmoides
Lepomis cyanellus
Lepomis microlophus
Lepomis megalotis
Lepomis macrochirus
Ambloplites rupestris
Pomoxis annularis
Stizostedion vitreum
Percina caprodes
Etheostoma jordani

IV. Species found in caves.

Typhlichthys subterraneus
Cottus carolinae

[1] Probably also belong in group II.

REFERENCES

BAILEY, REEVE M. 1940. *Hadropterus palmaris*, a new darter from the Alabama River system. *Jour. Wash. Acad. Sci.*, **30**(12): 524-530.

———1956. A revised list of the fishes of Iowa, with keys for identification. *In* Iowa Fish and Fishing by J. A. Harlan and E. B. Speaker. Iowa Conserv. Comm., pp. 327-377.

———, H. E. WINN, AND C. L. SMITH. 1954. Fishes of the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. *Proc. Acad. Nat. Sci. Phila.*, **106**: 109-164.

———, AND W. A. GOSLINE, 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. *Misc. Publ. Mus. Zool. Univ. Mich.* **93**: 1-44.

BEAN, TARLETON, H. 1884. On the occurrence of the striped bass in the lower Mississippi Valley. *Proc. U. S. Nat. Mus.*, **7**: 242-244.

BOSCHUNG, HERBERT T., AND A. F. HEMPHILL. 1960. Marine fishes collected from inland streams in Alabama. *Copeia*, **1960** (1): 73.

BROWN, JERRAM L. 1956. Identification and geographical variations of the cyprinodont fishes *Fundulus olivaceus* (Storer) and *Fundulus notatus* (Rafinesque). *Tulane Stud. Zool.*, **3** (7): 119-134.

BYRD, I. B. 1954. Here and there in conservation. *Alabama Conserv.*, **26** (1): 3, 26.

COOK, FANNYE A. 1952. Occurrence of the lamprey, *Lampetra aepyptera* in the Tombigbee and Pascagoula drainages, Mississippi. *Copeia*, **1952** (4): 268.

COOPER, L. B., AND A. F. HEMPHILL, 1957. Records of the lamprey *Lampetra aepyptera* from Alabama. *Copeia*, **1957** (1): 54.

CRAWFORD, RONALD W. 1954. Status of the bronze darter, *Hadropterus palmaris*. *Copeia*, **1954** (3): 235-236.

———1956. A study of the distribution and taxonomy of the percid fish *Percina nigrofasciata* (Agassiz). *Tulane Stud. Zool.* **4** (1): 1-55.

CROSS, FRANK B. 1953. Nomenclature in Pimephalinae, with special reference to the bullhead minnow, *Pimephales vigilax perspicuus* (Girard). *Trans. Kansas Acad. Sci.*, **56**: 92-96.

DENDY, JACK S., AND DONALD C. SCOTT. 1953. Distribution, life history, and morphological variations of the southern brook lamprey. *Ichthyomyzon gagei*. *Copeia*, **1953** (3): 152-162.

EDDY, SAMUEL. 1957. How to know the freshwater fishes. Wm. C. Brown Co., Dubuque, Iowa.

FOWLER, HENRY W. 1910. Notes on the variation of some species of the genus *Notropis*. *Proc. Acad. Nat. Sci. Phila.*, **62**: 273-293.

———1923. Records of fishes for the eastern and southeastern states. *Proc. Acad. Nat. Sci. Phila.*, **74** (1922): 1-27.

———1935. Notes on Georgia fishes — 1930 to 1933. *The Fish Culturist*, **15** (4): 72-74.

———1945. A study of the fishes of the southern Piedmont and Coastal Plain. *Monogr. Acad. Nat. Sci. Phila.*, **7**: 1-313.

GIBBS, ROBERT H. JR. 1957. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. III. Variation and subspecies of *Notropis venustus* (Girard). *Tulane Stud. Zool.*, **5** (8): 175-203.

———1957. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. I. Systematic status of the subgenus *Cyprinella*, with a key to the species exclusive of the *lutrensis-ornatus* complex. *Copeia*, **1957** (3): 185-195.

GILBERT, CHARLES H. 1891. Report of explorations made in Alabama during 1889, with notes on the fishes of the Tennessee, Alabama, and Escambia Rivers. *Bull. U. S. Fish Comm.*, **9** (1889): 143-159.

GUDGER, E. W. 1930. *Ichthyomyzon concolor* in the Coosa River at Rome, Georgia, with notes on other lampreys in our South Atlantic and Gulf drainages. Copeia, **1930** (4): 145-147.

HOWELL, HENRY H. 1957. A taxonomic and distributional study of the genus *Notropis* in Alabama. Unpublished Ph.D. dissertation, University of Alabama.

HUBBS, CARL L. 1927. *Micropterus pseudaplites*, a new species of black bass. *Occ. Pap. Mus. Zool. Univ. Mich.*, **184**: 1-15.

———1930. Materials for a revision of the catostomid fishes of eastern North America. *Misc. Publ. Mus. Zool. Univ. Mich.*, **20**: 1-47.

———1936. An older name for the black-nose dace. *Copeia*, **1936** (2): 124-125.

———, AND REEVE M. BAILEY. 1940. A revision of the black basses (*Micropterus* and *Huro*) with descriptions of four new forms. *Misc. Publ. Mus. Zool. Univ. Mich.*, **48**: 1-51.

———, AND JOHN D. BLACK. 1947. Revision of *Ceratichthys*, a genus of American cyprinid fishes. *Misc. Pub. Mus. Zool. Univ. Mich.*, **66**: 1-56.

———, AND KARL F. LAGLER. 1947. Fishes of the Great Lakes Region. *Bull. Cranbrook Inst. Sci.*, **26**: 1-186.

———, AND MILTON B. TRAUTMAN. 1937. A revision of the lamprey genus, Ichthyomyzon. *Misc. Publ. Mus. Zool. Univ. Mich.*, **35**: 1-109.

JORDAN, DAVID STARR. 1877a. A partial synopsis of the fishes of upper Georgia. *Ann. N. Y. Lyceum Nat. Hist.*, **11** (1876): 307-377.

———1877b. Contributions to North American Ichthyology. II. A. Notes on Cottidae, Etheostomatidae, Percidae, Centrarchidae, Aphododeridae, Dorysomatidae and Cyprinidae, with revisions of the genera and descriptions of new or little known species. *Bull. U. S. Nat. Mus.*, **10**: 1-68.

———1878. Contributions to North American Ichthyology. III. B. Synopsis of the family Catostomidae. *Bull. U. S. Nat. Mus.*, **12**: 97-230.

———1879. On the distribution of fresh-water fishes of the United States. *Ann. N. Y. Acad. Sci.*, **1**: 92-120.

———1929. Manual of the vertebrate animals of Northeastern United States inclusive of marine species. (13th. ed.). World Book Co., Yonkers, N. Y.

———, AND ALEMBERT W. BRAYTON. 1878. Contributions to North American Ichthyology. III. A. On the distribution of the fishes of the Allegheny region of South Carolina, Georgia, and Tennessee, with descriptions of new and little known species. *Bull. U. S. Nat. Mus.*, **12**: 3-95.

———, AND HERBERT E. COPELAND. 1877. Check list of the fishes of the fresh water of North America. *Bull. Buffalo Soc. Nat. Sci.*, **3** (1875-1877): 133-164.

———, AND BARTON W. EVERMANN. 1896-1900. The fishes of North and Middle America, pts. 1-4. *Bull. U. S. Nat. Mus.*, **47**: 1-3313.

———, BARTON W. EVERMANN, AND HOWARD W. CLARK. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the boundary of Venezuela and Colombia. *Rept. U. S. Fish. Comm.* (1928), **2**: 1-670.

———, AND CHARLES H. GILBERT. 1883. Synopsis of the fishes of North America. *Bull. U. S. Nat. Mus.*, **16** (1882): 1-1018.

LAGLER, KARL L. 1956. Freshwater Fishery Biology. Wm. C. Brown Co., Dubuque, Iowa.

MILLER, ROBERT RUSH. 1955. An annotated list of the American cyprinodontid fishes of the genus *Fundulus*, with the description of *Fundulus persimilis* from Yucatan. *Occ. Pap. Mus. Zool. Univ. Mich.*, **568**: 1-25.

MOORE, G. A. 1957. Fishes. *In* Vertebrates of the United States. McGraw-Hill Book Co., New York.

RANEY, EDWARD C. 1952. A new lamprey, *Ichthyomyzon hubbsi*, from the upper Tennessee River system. *Copeia*, **1952** (2): 93-99.

SCOTT, DONALD C. 1951. Sampling fish populations in the Coosa River, Alabama. *Trans. Amer. Fisher. Soc.*, **80** (1950): 28-40.

SMITH, ROBERT E. 1960. A survey of the fishes of Big Sandy Creek and its tributaries, Tuscaloosa County, Alabama. Unpublished Master's thesis, University of Alabama.

SUTTKUS, ROYAL D., AND EDWARD C. RANEY. 1955a. *Notropis baileyi*, a new cyprinid fish from the Pascagoula and Mobile Bay drainages of Mississippi and Alabama. *Tulane Stud. Zool.*, **2** (5): 71-86.

———1955b. *Notropis asperifrons*, a new cyprinid fish from the Mobile Bay drainage of Alabama and Georgia, with studies of related species *Tulane Stud. Zool.*, **3** (1): 3-33.

TAYLOR, WILLIAM RALPH. 1954. Records of fishes in the John N. Lowe Collection from the Upper Peninsula of Michigan. *Misc. Publ. Mus. Zool. Univ. Mich.*, **87**: 1-50.

———1957. A revision of the genus *Noturus* Rafinesque with a contribution to the classification of the North American catfishes. *Dissertation Abstr.*, **17** (1): 1-192.

WOODS, LOREN P., AND ROBERT F. INGER 1957. The cave, spring and swamp fishes of the family Amblyopsidae of Central and Eastern United States. *Am. Midl. Nat.*, **58** (1): 232-256.

Phenology of Sumacs[1]

ELIZABETH F. GILBERT
Oberlin College, Oberlin, Ohio

ABSTRACT: The nature and extent of phenological variability among individuals of sumac, *Rhus glabra*, was investigated.

The phenological events considered are: bud elongation, bud opening, leaf appearance, cessation of leaf and twig growth, inflorescence appearance, first flower and fruit, and cessation of inflorescence growth. The sex of the clone, height of the stem above ground, age of the stem, and the final twig length showed association with phenological events.

Phenological stages are grouped into the cessation events which develop slowly throughout the clone, and the developmental events which occur rapidly throughout the clone.

Through the use of a multiple range test, the mean values of all clones for each event can be grouped into those which show no statistical difference from each other. The number of times one clone is grouped with another may be considered an index of the phenological similarity of the clones.

The major conclusions drawn are: (1) the phenological variability appears to be primarily associated with the genetic constitution of the plant; (2) aspects of the structure and life history of the clone seem associated to a lesser extent with its phenology; (3) exposure of the clone on the hilltop and exposure of the stem within the clone seem to have no effect on the phenology.

INTRODUCTION

There is often a difference in the time of appearance of developmental stages of different species and of different individuals of a species. Plant phenology is the study of the responses of plants to periodic changes in their environment. Though many observations have been made on the date of occurrence of certain events in the life of a plant, such as, leafing, flowering, maturation of fruit, acquisition of autumn color, or leaf-fall, there have been few studies directed toward an understanding of the extent and causes of such intraspecific variability.

An attempt has been made in this study to describe the phenological variability of two sumacs, *Rhus glabra* and *Rhus typhina*, and to understand the causes of this variability. These species were chosen for three reasons: prevalence in Washtenaw County, Michigan, short stature, and their clonal habit. The common occurrence made it possible to find suitable material with some degree of ease, whereas, their usual short stature enables detailed observations to be made on all parts of the plant. The clonal habit of growth, spreading under-

[1] I am indebted to Dr. Stanley A. Cain for his advice and encouragement throughout the course of this study. The statistical assistance of Dr. Don W. Hayne is much appreciated, and financial assistance from the Botanical Gardens of the University of Michigan and from the Graduate Student Research Fund of the Horace H. Rackham School of Graduate Studies made this work possible.

ground from one original plant, gives the same genetic constitution, with the exception of possible bud sports, to many stems covering a large area.

Preliminary studies where carried out on 48 clones of *Rhus*, 18 of which were classified as *Rhus typhina*, 6 as *Rhus glabra*, and 24 as intermediates between them. The sites of clonal growth were chosen to represent as wide an environmental variety as possible. The results of observations on the occurrence of eight phenological stages show that variation does exist in the phenology of *Rhus*. The three taxonomic groups, *Rhus glabra*, *Rhus typhina*, and the intermediate *Rhus*, exhibited responses which were much alike. Analyses of variance suggested that there might be an association between the site and some of the phenological events. Possible association between the growth of sumac and rainfall or temperature was so faint as to suggest that microclimatic studies would be necessary for further study.

During the following season, detailed observations were centered upon nine clones of *Rhus* which appeared very similar morphologically. Seven clones were carpellate, and two were staminate. All had little or no pubescence on the twigs, and the carpellate clones showed only clavate or cigar-shaped hairs on the fruit. The clones were thus considered to be *Rhus glabra*, in a wide sense, or in a strict sense, an intermediate *Rhus*, but very close to *Rhus glabra*.

The nine clones chosen for observation were considered distinct entities by virtue of physical separation from other clones and by morphological characters (chiefly pubescence of the twigs and fruits, branching angles, and height of the stem) which made for ready recognition of each clone. The clones were located on the top and on the north, south, and west flanks of a hill in the northwest portion of Washtenaw County, Michigan.

METHODS

Preparation for field work.—A topographic map with five-foot interval contour lines served as the base for the selection of sample areas within the nine clones. Reference stakes were set out in each clone and added to the map by triangulation and by measurement. Each clone was then mapped about its reference points, and the map was transferred to squared paper on which the contour lines were drawn. The scale of the map was such that each square of 3/16 inch represented one square meter. In addition to the outline of the clone, the height of the stems was added to the map as isochores of stem height. The clone was divided into four sectors centered on the tallest portion of the clone by north, south, east, and west radii. A sample section of the clone was designated by lines representing topography, height of stem, and exposure within the clone. The number of sample sections varied from 6 to 21 with variation in height and topography. The squares within each sample section were numbered, and, with a table of random numbers, one square was selected as the sample area.

Each sample area was located in the field by reference to the stakes. Within an area three sample stems were selected, using a table of random numbers. One sample twig of the previous year's growth was selected, again by using a table of random numbers. In this manner three sample twigs on three different sample stems were tagged in each sample section of each clone. The descriptions of the clones are summarized in Table I.

Phenological field methods.—Measurements were made of the dormant buds on each tagged twig, and the twig was observed on alternate days until the buds began to elongate. The bud which elongated most rapidly was tagged for future study, and measurements were made on alternate days until daily growth increments increased to more than one millimeter.

The date on which the bud was first observed to lengthen was termed "bud elongation" and is the first event recorded in the phenological summary, Table II. As the bud lengthened, the leaves first elongated with the bud and gradually bent off at an angle from the mass of the bud. When a leaf bent away from the main portion of the bud so that the tip of the leaf was separated from the main portion, the date was noted and the event was called "bud opening." This leaf was tagged and observed at subsequent visits. With further lengthening of the bud, other leaves became distinct until it was possible to see the new twig within the bud. The day on which this occurred was recorded as "leaf appearance" in the phenological summary. When the twig became visible, measurements were no longer made of the length of the bud. After leaf appearance, the length of the leaf was recorded. The length of the twig, from the base of the original bud to the base of the young leaves which mask the growing tip, was also noted. When the inflorescence appeared, measurements of the twig were made to the base of the first branch of the inflorescence. The day upon which it was possible to see the young inflorescence in the field was recorded as "inflorescence appearance." When it was possible to look into a flower, the date was noted as "first flower." The date of the first fruit was more subjective, since the swelling of the ovary was so gradual. In some flowers, the fruit hairs were easily seen to develop, and sometimes these hairs acquired a brilliant red color while the ovary was scarcely enlarged. In other fruits, however, the hairs of the fruit remained colorless for a longer period. The date of the "first fruit" was considered to occur when the ovary showed an apparent increase in size.

Measurements were made of the lengths of the leaf, twig, and inflorescence on each day during the season of rapid growth. When one measurement had remained similar for six days, the organ was not measured again until several days later. When the measurements had remained similar for 18 days (in the case of twigs and leaves) or for 10 days (in the case of inflorescences), growth of that organ was considered to have ceased and measurements were discontinued. The first day on which the final length was recorded was noted as

the day of cessation of growth in length of the twig, leaf, or inflorescence. (For the sake of brevity, the cessation of growth in length of the twig will be referred to as "twig cessation," and similarly, "leaf cessation" and "inflorescence cessation.")

TABLE I.—Descriptions of clones

Clone	Sex	Location on hill	Age of sample stems (yrs)	Sample stem height (m)	No. of sample sections	Clone extent (m)
A	F	SW slope	2-10	0.4-2.0	18	25 x 40
B	F	SE slope	4-13	0.4-2.0	21	30 x 30
C	F	Hilltop	1-13	0.4-2.5	16	24 x 25
D	F	Hilltop	4-13	1.1-3.0	8	17 x 25
E	F	NE slope	4-13	0.4-2.0	11	15 x 16
F	F	NW slope	5-11	0.4-2.5	13	13 x 17
G	F	W slope	3-11	0.4-2.5	14	20 x 20
H	M	W slope	4-9	0.4-1.5	6	15 x 15
I	M	Hilltop	2-11	0.4-2.0	15	28 x 36

TABLE II.—Phenological summary

Clone	Dates	Range No. of days	Mean	Standard Deviation
		Bud Elongation		
A	4/26-5/12	17	5/1	4.04
B	4/26-5/16	21	5/4	6.04
C	4/26-5/28	33	5/2	6.57
D	4/28-5/20	23	5/1	3.00
E	4/28-5/13	16	5/2	4.02
F	4/28-5/31	34	5/1	3.92
G	4/28-5/6	9	4/30	2.68
H	4/28-5/2	5	4/29	1.88
I	4/28-5/14	17	5/6	4.59
		Bud Opening		
A	5/12-5/18	7	5/14	1.79
B	5/12-5/18	7	5/15	1.63
C	5/10-6/5	27	5/15	4.62
D	5/12-5/17	6	5/14	1.39
E	5/13-5/17	5	5/14	1.00
F	5/13-5/28	16	5/16	2.46
G	5/13-5/17	5	5/15	0.29
H	5/14-5/18	5	5/15	1.21
I	5/13-5/23	11	5/16	1.63
		Leaf Appearance		
A	5/12-5/30	19	5/16	2.79
B	5/13-5/21	9	5/17	1.68
C	5/12-5/31	20	5/16	4.37
D	5/15-5/20	6	5/16	1.17

TABLE II.—(continued)

Clone	Range Dates	Range No. of days	Mean	Standard Deviation
E	5/15-5/20	6	5/16	1.11
F	5/15-5/31	17	5/18	2.74
G	5/16-5/20	5	5/17	1.10
H	5/16-5/17	2	5/16	0.29
I	5/14-5/21	8	5/17	1.49
	Cessation of Leaf Growth			
A	5/23-6/20	29	6/8	7.60
B	5/26-7/9	45	6/14	9.72
C	5/30-7/1	33	6/10	9.27
D	6/4-6/27	24	6/14	7.19
E	5/21-7/10	51	6/9	8.44
F	6/5-7/1	27	6/14	7.51
G	6/3-7/4	32	6/13	8.39
H	5/28-6/21	25	6/7	6.48
I	5/25-7/9	46	6/13	9.97
	Cessation of Twig Growth			
A	6/9-7/4	26	6/20	6.63
B	5/22-7/4	44	6/18	7.07
C	6/7-6/28	22	6/19	6.72
D	5/18-7/11	55	6/15	14.13
E	6/1-7/3	33	6/18	7.37
F	5/28-7/13	47	6/20	7.78
G	6/2-7/5	34	6/17	7.17
H	6/14-7/6	23	6/23	7.47
I	6/2-7/3	32	6/21	5.91
	Inflorescence Appearance			
A	5/25-6/5	12	5/30	2.34
B	5/22-6/1	11	5/30	2.09
C	5/23-6/18	27	5/31	6.93
D	5/27-6/4	9	5/31	2.28
E	5/23-6/6	15	5/31	2.88
F	5/30-6/8	10	6/1	2.04
G	5/27-6/11	16	6/1	2.74
H	5/24-6/2	10	5/29	2.20
I	5/23-6/1	10	5/28	2.57
	First Flower			
A	7/1-7/9	9	7/4	1.73
B	6/27-7/7	11	7/3	2.09
C	6/27-7/13	17	7/2	4.08
D	7/2-7/6	5	7/4	1.23
E	7/1-7/6	6	7/3	1.21
F	7/1-7/9	9	7/3	1.53
G	7/1-7/6	6	7/3	1.16
H	6/30-7/3	4	7/2	1.00
I	6/26-7/7	12	7/1	1.87

TABLE II.—(continued)

Clone	Dates	Range No. of days	Mean	Standard Deviation
		First Fruit		
A	7/6-7/12	7	7/10	1.42
B	7/6-7/11	6	7/9	1.61
C	7/2-7/19	18	7/8	4.41
D	7/9-7/15	7	7/12	2.03
E	7/8-7/10	3	7/9	0.34
F	7/5-7/11	7	7/8	1.56
G	7/8-7/13	6	7/10	1.29
H	(male)			
I	(male)			
		Cessation of Inflorescence Growth		
A	6/18-7/15	28	7/2	5.66
B	6/19-7/12	24	6/28	4.89
C	6/25-7/19	25	7/5	6.61
D	6/28-7/13	16	7/3	4.68
E	6/21-7/19	29	7/5	7.01
F	6/19-7/11	23	7/1	4.85
G	6/22-7/19	28	7/9	8.75
H	6/27-7/13	17	7/4	3.84
I	6/26-7/11	16	7/3	2.93

RESULTS

The dates of nine phenological events are recorded in Table II.

The raw phenological data consist of daily records of the length of the selected twigs, leaves, and inflorescences and of notes of the dates of opening of the bud and the appearance of the leaf, the inflorescence, the first flower, and the first fruit. The complete data are held by the writer and may be consulted.

The first event of the season, bud elongation, took place over a period of from five days in clone H to 34 days in clone F. The average date of bud elongation varied from April 29th in clone H to May 6th in clone I.

Bud opening followed shortly after the initiation of growth in length, and usually all sample twigs in one clone opened within a period of a few days. The buds of the sample twigs of clones E, G, and H opened in five days, but buds of clone C opened over a period of 27 days. The average date of bud opening was from May 14th to 16th, a relatively short span of time.

Leaf appearance in clone H took place on two days, whereas all leaves studied in clone C required 20 days for appearance. The average dates of leaf appearance exhibit a range of only three days, from May 16th through May 18th. The earliest average date is May 16th and the latest May 18th.

Cessation of leaf growth occupied a much longer time in each clone, from 24 days in clone D to 51 days in clone E. The average date of cessation of leaf growth ranged from June 7th in clone H to June 14th in clones B, D, and F.

Cessation of twig growth also occurred over a long period of time; in clone C, 22 days, and in clone D, 55 days. The average dates of cessation of twig growth occurred over only eight days, from June 15th in clone D to June 23rd in clone H.

Appearance of the inflorescence on all sample twigs occurred in clone D in nine days and in clone C in 27 days. The average date of inflorescence appearance ranged from May 28th in clone I to June 1st in clones F and G.

The appearance of the first flower occurred in a relatively short time, from a range of four days in clone H to 17 days in clone C. The average dates are close together, from the 1st of July in clone I to the 4th of July in clones A and D.

The seven carpellate clones set fruit within a relatively brief period of from three days in clone E to 18 days in clone C. The earliest average date of appearance of the first fruit was July 8th in clones C and F, and the latest average date was July 12th in clone D.

The cessation of inflorescence growth, like the cessation of growth of the leaf and the twig, covered a longer period of time. Clone D exhibited the shortest range with 16 days, and clone E's cessation of inflorescence growth extended over 29 days.

The similarity of the three events — leaf cessation, twig cessation, and inflorescence cessation, and their differences from the other six phenological events — was suggested by the ranges and means in

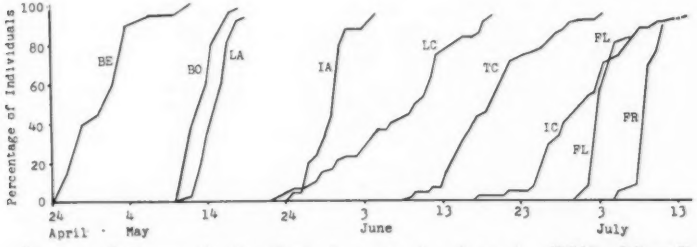


Fig. 1.—Progress of phenological events in clone A. KEY: BE = Bud elongation; BO = Bud opening; LA = Leaf appearance; IA = Inflorescence appearance; LC = Cessation of leaf growth; TC = Cessation of twig growth; FL = First flower; FR = First fruit; IC = Cessation of inflorescence growth.

Table II. The similarity among these events may be more easily seen in Figures 1 and 2 in which the percentage of the sample individuals in one clone which have undergone the specified event are plotted against time. Each series of curves represents the nine events of one

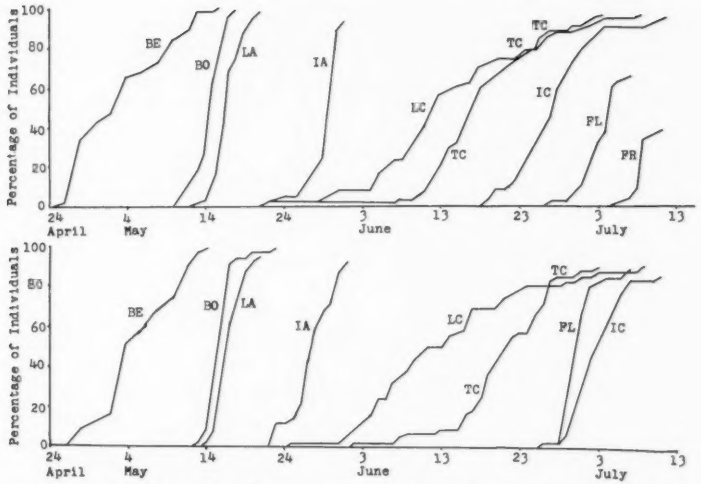


Fig. 2.—Progress of phenological events in clones B, above, and I, below.

clone, and the curves of three clones are shown as examples. The three "cessation" events usually occur over a longer period than the developmental events. The cessations progress more slowly in the clone than do the other events. (The gradually diminishing total represented by the diminishing height of the curves reflects the incomplete development of certain twigs.)

A comparison of the development of one event in one clone with the same event in other clones shows a great similarity between different clones. In most clones, the majority of the buds of the sample twigs elongated within a few days. The most notable exception to this rapidity in development was clone I which showed buds beginning to elongate over a two-week interval. In clones C, D, and F, the duration of bud elongation is lengthened greatly by only a very few individuals. In two clones, G and H, bud elongation was completed before bud opening was initiated. In the remaining clones, bud elongation was essentially complete before the first buds opened. In all clones, the progress of bud opening throughout the clone was similar in its rapidity of development in the clone. Leaf appearance was almost completed in all clones before any of the inflorescences appeared. The appearance of the inflorescence occurred on all stems of a clone within a few days. A few days before or after the appearance of the first inflorescence, a few leaves stopped growing. In some instances (clones A and E) some cessation of leaf growth preceded the appearance of the inflorescence. Cessation of twig growth also began at about this time, in clones D and F, preceding both the first inflorescence appearance and the first leaf cessation. The cessation of twig growth of clone G began before the leaf growth cessation of

that clone. The first inflorescence growth cessation preceded the appearance of the first flower. The progress of inflorescence growth cessation was slow, however, so that both the first flower and the first fruit had appeared in each clone before the last inflorescence had ceased to grow. (In clone F, however, the appearance of the fruit and the cessation of inflorescence growth occurred on the same day.) The first inflorescence growth cessation, first flower, and first fruit usually occurred before twig growth cessation was completed.

Figures 1 and 2 show that there are two types of progress of an event in a clone; rapid, as in bud elongation, bud opening, leaf appearance, first flower, and first fruit, and slow, as in leaf, twig, and inflorescence growth cessation.

ANALYSIS OF PHENOLOGICAL MEANS

The average dates of the different clones for the different phenological events are observed to vary; to determine which variations are significant, Kramer's (1956) modification of a multiple range test was employed. This test permits the grouping of the mean values into those which are and are not significantly different. The means of the clones, represented simply by the clone letter, are arranged in order from early to late. Means which are underlined by the same line are not significantly different, whereas those means not underlined by the same line do differ significantly.

Bud elongation	I B E A C F D G H
Bud opening	I F B G C H D E A
Leaf appearance	F B I G D C E H A
Leaf cessation	B F D G I C E A H
Twig cessation	H I F A C B E G D
Inflorescence appearance	F G E C D A B H I
First flower	A D B G E F H C I
First fruit	D A G E B F C
Inflorescence cessation	G C E H D I A F B

The means which are not statistically different from each other vary from one phenological event to another. An index of the phenological similarity of the clones may be found by investigating the number of times one clone was considered not statistically different from another. Clones C and D and clones C and E show the greatest phenological similarity, since their means are not statistically different in 13 instances. Clone I is least like the other clones phenologically.

The means of the clones for each of the phenological events give a method of designating a clone as "early," "mid," or "late" in comparison with the other clones. If the mean values for all the clones for each event are ranked from early to late, the number of times a clone appears in a certain relative order may be tabulated. (The appearance of the first fruit was not considered, since the two staminate clones did not form fruits.) Clone I, for example, appears among the earliest three clones four times, among the middle three clones twice, and among the latest three clones twice. On the basis of this information, clone I is called an "early" clone. "Early" clones are: B, F, and I; "mid" clones are C and G; and "late" clones are A, D, E, and H.

Data on the age, height, and location of the sample twigs were plotted against different phenological events. The resulting scatter diagrams showed suggestions of both positive and negative correlations, therefore a series of analyses of variance was completed (Table III).

TABLE III.—Analyses of variance

	Classes between or among which analyses were run					
Analysis	All clones	Height classes (0.5 m)	Exposure within clone	Age	Sex	Final twig length
Bud Elongation	1%*	NS*	NS	5%*	1%	1%
Bud Opening	1%	5%	NS	1%	1%	1%
Leaf Appearance	1%	5%	NS	1%	1%	1%
Leaf Growth Cessation	1%	NS	NS	1%	NS	NS
Twig Growth Cessation	5%	NS	NS	NS	5%	1%
Inflorescence Appearance	1%	NS	NS	NS	1%	1%
First Flower	1%	NS	NS	NS	1%	NS
First Fruit	1%	1%	1%	NS	..	NS
Inflorescence Growth Cessation	1%	NS	NS	NS	NS	1%

* 1%, significant at 1% level
5%, significant at 5% level
NS, not significant at 5% level

Among all clones, there is significant or highly significant difference for all phenological events. Among the half-meter height classes, there is one event which is statistically highly significant and two events which are significant. Exposure within the clone shows no

statistical significance save in the appearance of the first fruit. Some phenological events are recorded as statistically highly significant and some as statistically not significant when the data are analysed by age groups. Four phenological events are found to be highly significant when information is grouped by sex. Among final twig length classes, six events appear to be highly significant statistically and three not statistically significant.

DISCUSSION

PHENOLOGICAL EVENTS

The earliest event, bud elongation, is one of six which progress rapidly through a clone when once it has begun. Bud elongation, because it is the earliest, is most likely to be affected by changes in the weather during the early portion of the growing season, since it is likely that the weather may be the controlling factor of the environment at that time. Consequently the curve of progress of bud elongation through a clone shows a rapid rate of development interrupted by plateaus which may correspond with periods when the weather was unfavorable for development. The span of time needed for this event to occur, therefore, is greater than the duration of the other five "rapid" events. In analyses of variance, sex and final twig length appeared to show highly significant association with bud elongation. Age appeared to show significant association, and height of stem and exposure within the clone showed no significant association with elongation.

Bud opening is initiated 10 to 16 days following the start of bud elongation in a clone. One of the most rapidly developing events, bud elongation will be observed on all sample stems of a clone often within four days of the first appearance of that event within the clone. Through analyses of variance, age, sex, and final twig length show a highly significant association with bud opening. Significant association is indicated in the case of height, and no significance could be found to be associated with exposure within the clone.

Leaf appearance, like bud opening, is a rapidly progressing event in all clones. There is great similarity from clone to clone in the shape of the curves representing the bud opening and leaf appearance. Only a few days separate leaf appearance from bud opening. Analyses of variance show that age and final twig length have highly significant association with leaf appearance. Significant association appears with height, and no significance is found with sex and exposure within the clone.

Leaf growth cessation is one of the events which progresses slowly through a clone. One may postulate that the causes of initiation of development are of a different nature than the causes of cessation of development and that this is shown by the different nature of the progress of such events in a clone. Though leaf growth cessation usually first appears in a clone following the appearance of the last

leaf of the sample twigs, it is possible, and indeed occurred in clones A and C, for certain leaves to cease growing even before other leaves have appeared. From analyses of variance, one may say that there is a statistically highly significant association with leaf cessation by age, and that no significance may be attached to height, exposure within the clone, sex, or final twig length.

The appearance of the inflorescences in a clone was first noticed at approximately the same time as the first cessation of leaf growth. Leaf growth cessation developed slowly through a clone, whereas the inflorescences appeared within a short time throughout the clone. The rate of progress of inflorescence appearance closely parallels the rate of progress of bud opening and leaf appearance. The sex of the clone and final twig length show statistical evidence of an association with inflorescence appearance. No statistical significance was attached to height, age, or exposure within the clone.

The cessation of growth of the sample twigs in any one clone takes place over a relatively long period of time. The rate of progress within a clone is similar to that of the cessation of leaf growth. In most instances the first cessation of twig growth occurs several days after the first leaves have ceased to grow in that clone, though in clones D, F, and G, the cessation of twig growth appears before the cessation of leaf growth is initiated. In clone D, cessation of twig growth was initiated even before the first inflorescence appeared. Final twig length appears to show highly significant association with twig cessation, the sex of the clone appears to be of significance, whereas the height, age, and exposure within the clone show no statistical significance.

The cessation of growth of the inflorescence is the next event to appear in a clone, though like the cessation of growth of the twig and the leaf, it is an event which develops slowly through the clone. The curve representing the progress of the event shows a rate of development similar to the rate of progress of the cessation of growth of the leaf and the twig. Final twig length appears to have a highly significant association with the cessation of growth of the inflorescence, whereas no significant association can be shown in the cases of the height, age, sex, and exposure within the clone.

Flowering and fruiting both follow the first cessation of growth of the inflorescence and develop rapidly in the clone, once they have begun. The interval between the appearance of the first flower and the appearance of the first fruit is remarkably constant, approximately one week. Analyses of variance show that there appears to be a highly significant association of the sex of the clone with its date of first flowering, but no statistically significant association with height, age, final twig length, and exposure within the clone. No statistical significance is seen with age or final twig length.

The most remarkable feature of *Rhus* phenology is the similarity of events from clone to clone. The relative time of appearance and rate of progress of the event is much the same for all clones.

The phenological events are of two types, initiation events, which develop rapidly within a clone, and cessation events, which develop slowly within a clone.

PHENOLOGY OF THE CLONES

The series of phenological phases of one clone follow each other at intervals which are fairly uniform from clone to clone. Within one clone, one event is usually essentially completed before the next is initiated. The cessation events overlap others more often than do the developmental ones.

When the average values for all clones for each event are grouped together, the clones which fall together cannot be said to be statistically the same, but are said to be not statistically different. Clones C, D, and E which are often grouped together may be said to respond to similar environmental factors in a phenolcgically similar manner. Clones G and H represent another group which shows some phenological similarity. Clone B does not appear very similar to others in phenology, but may be said to be phenologically intermediate between clones G and H and clones F and A, which tend to respond in a similar manner phenologically. Clone I is least often associated with others in terms of the phenological responses. Apparently phenological similarity is but one manifestation of physiological and genetic similarity and similar phenological responses may be used as another criterion in attempting to determine the taxonomic position of a plant.

Aspects of the structure and life history of a clone show a varying association with its phenology. Though in four events the age of the stem appears to show a significant association, yet other events seem unassociated with age. The height of the stem above ground appears to have significance in three events, and these events share two in common with those significantly associated with age. The sex of the clone appears to have a significant association with six events, but no association with two others. Similarly, the final twig length may bear an association with six events. Exposure within the clone appears to be of significance in only one instance, yet the fact that the appearance of the first fruit is significantly associated with exposure within the clone perhaps is more of a coincidence than an evidence of a direct association.

By studying clones located on and about one hilltop, some variation in the environment was assured. There appears to be no correlation with position on the hill, however, although an analysis of variance shows significant difference among all clones for all phenological events. Among the clones ranked as "early," one finds a southerly exposure, a northerly exposure, and one level clone represented. Similarly among those clones considered "late," one grows on a southerly and one on a northerly slope. This would indicate that whatever the factors of the environment may be which differ from a north to a south exposure, they have no observable effect on the phenology of these sumacs. The significant difference shown

among the clones by the analyses of variance must therefore be caused by genetic differences among the clones.

There can be little comparison drawn between the present study and previous work in plant phenology. This study is an outgrowth of previous attempts to find a correlation between phenology and environmental factors. Previous work has attempted to find phenological correlations with temperature (Brendel, 1859), moisture (Hiley and Cunliffe, 1922), and light (Leibundgut, 1954). The present study has made no attempt to state the precise temperature, light, or moisture regime which the observed clones have undergone.

Clausen and Hiesey (1958) have shown that though the order of bloom of flowers in a transplant garden may vary from the order under natural conditions, yet the order of bloom remains constant from year to year. McMillan and Pagel (1958), working with *Symphoricarpos,* found that those clones which tended to be early or late in their natural habitat frequently retained this characteristic in a common garden. The work of Morris, Silen, and Irgens-Moller (1957) with the bursting of Douglas-fir buds also points out the hereditary nature of the prime control of plant phenology. The present study substantiates the primary importance of heredity in controlling events in the sumacs.

CONCLUSIONS

The phenological variability which exists in local species of sumac, *Rhus glabra, Rhus typhina,* and intermediates between the two, is not controlled by any one factor, though the most important control over their phenology is exercised by the genetic constitution of the plant. To a lesser extent, the structure and life history of the plant seem to affect its phenology. The sex of the clone, the height of the stem above ground, the age of the stem, and the final twig length show association with some of the phenological events. The events affected are not the same in each instance, though the opening of the bud was associated with all four characters; sex, height, age, and final twig length. Only the exposure of the clone in relation to the hill and the exposure of the stem within the clone seem to have no effect on the phenology of these sumacs.

Phenological events are of two types, those which are soon completed throughout the clone, the rapidly developing events, and those which are slow in developing. Those events which mark the initiation of development of an organ are of the rapid type, and the events dealing with the cessation of growth of an organ are those which occur over a long period of time.

The phenological responses of clones to their environment offer a means of segregating the clones into those which react similarly to similar situations. The phenological similarity of clones may be considered as an expression of the physiological and genetic similarity of the individuals and hence may be used as a measure of the relationship of individuals.

REFERENCES

BRENDEL, FREDERICK 1859. On meteorology in connection with botanical investigations. *Illinois State Agric. Soc. Trans.*, **3**:671-675.

CLAUSEN, JENS AND WILLIAM M. HIESEY 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. *Carnegie Inst. Wash. Publ.*, 615. vii + 312 p.

HILEY, W. E. AND NORMAN CUNLIFFE 1922. An investigation into the relation between height growth of trees and meteorological conditions. *Oxford Forestry Memoirs*, 1. 19 p.

KRAMER, CLYDE YOUNG 1956. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics*, **12**:307-310.

LEIBUNDGUT, H. 1954. Zur Phänologie der Laubbäume, insbesondere der Buche. 2. Mitteilung. *Schweiz. Zeitschr. Forstw.*, **105**(5/6):296-302.

MCMILLAN, CALVIN AND BEVERLY F. PAGEL 1958. Phenological variation within a population of *Symphoricarpos occidentalis*. *Ecology*, **39**:766-770.

MORRIS, WILLIAM G., R. R. SILEN AND H. IRGENS-MOLLER 1957. Consistency of bud bursting in Douglas fir. *J. Forestry*, **55**:208-210.

Habitat Selection and Activity of the Wood Frog, Rana sylvatica Le Conte

HAROLD HEATWOLE
University of Puerto Rico, Rio Piedras

ABSTRACT: On the basis of field and laboratory studies, I found that the habitat selected by *Rana sylvatica* in the non-breeding season is one combining a forest canopy and small ponds. Frogs face the water and sit at the edge of the bank on flat, recently submerged litter. They follow the receding water-line as the ponds dry up and move under the loose leaf-litter of the forest floor when the water is gone.

Within the range of field conditions, more frogs are active at high temperatures and relative humidities than at lower ones. They are sedentary and even during "activity" periods are motionless unless they see a prey item or are disturbed.

The typical escape behavior is to dive in a pond and either become concealed in submerged litter or surface some distance away.

INTRODUCTION

Within the geographic range of a species, neither individuals nor populations are uniformly distributed. They may be absent from some habitats because one or more environmental factors exceed their tolerance limits or because they are eliminated by competition with other species. However, local distribution may also be greatly influenced by behavioral responses to various components of the environment which tend to keep the animals within certain types of situations. These responses are collectively known as habitat selection.

The wood frog, *Rana sylvatica*, occurs from Alaska to Georgia and from Labrador to British Columbia and occupies a diversity of habitats including boreal conifer forests, swamps, and upland forests such as oak-hickory and beech-maple. Low temperatures limit its geographic distribution on the north, high ones limit it on the south and oceans are barriers on the east and west (Martof and Humphries, 1959). However, the factors affecting distribution of wood frogs within their geographic range have previously been poorly understood. This paper reports on a study of habitat selection in this species made in southern Michigan from late March to early June, 1957 and 1958, and September and October, 1958.

Acknowledgment:—I am particularly indebted to Prof. F. H. Test of the University of Michigan for his valuable aid, encouragement, and criticism. Drs. C. F. Walker, W. R. Murchie, and S. H. Spurr, all of the University of Michigan, and Dr. Edward Bellis of Pennsylvania State University read the manuscript and offered helpful advice. The National Science Foundation provided predoctoral fellowships during the tenures of which the project was carried out. The Argus Camera Company and the University of Michigan permitted the use of their properties for the study. My wife, Audry, assisted in the field and in preparation of the manuscript.

DESCRIPTION OF THE STUDY AREA

The study area was a tract of land in Washtenaw Co., Michigan (Webster Township, T.1S., R.5E., S.1) characterized by gently rolling hills separated by marshes, bogs and swamps. Some of the higher areas are abandoned fields and pastures; others maintain oak-hickory stands. Two types of swamp occur; one contains chiefly *Picea mariana* and *Larix laricina*, whereas the other consists of hardwoods. A more detailed description of the area is given by Heatwole and Getz (1960) and Getz (1961).

Most of the investigation was carried out in the hardwood swamp as it was the only habitat supporting a large population of wood frogs. Its dominant plants were *Ulmus americana, Acer rubrum,* and *Betula lutea.* The canopy was relatively open and the shrub layer not well developed, although *Rhus vernix, Ilex verticilata,* and young dominants were occasionally present. The herbaceous layer consisted chiefly of ferns (*Osmunda regalis, Osmunda cinnamomae, Onoclea sensibilis, Dryopteris spinulosa*), skunk cabbage (*Symplocarpus foetidus*) and mosses. Less common ground-layer plants were *Caltha palustris, Coptis groenlandica, Trientalis borealis, Maianthemum canadense, Boehmeria cylindrica, Impatiens capensis,* and *Vaccinium angustifolium.* The substrate was Rifle Peat (Veatch *et al.*, 1930), a black, mucky soil consisting chiefly of organic matter. Two soil samples gave pH values of 5.2 and 4.8.

Different parts of the hardwood swamp varied in ground vegetation, topography of the forest floor, and density of canopy. Accordingly, the area was divided into three sections, hereafter designated as the northern, middle and southern sections. The northern section had a more open canopy and denser herb stratum than the southern one. The most conspicuous difference among the three areas, however, was relief of the forest floor. In the northern section there were scattered depressions which were filled with water in the spring and early summer. Mounds surrounded the bases of trees. By contrast, the southern section had a relatively flat floor and contained fewer mounds and depressions. The middle section was intermediate in all respects.

The forest floor of the swamp was classified into several categories on the basis of moisture conditions and litter structure. They were: 1) open water; 2) areas of standing water choked with partly floating leaves; 3) emergent areas which had been previously inundated and on which the leaves were limp, soft and partly decayed, forming a compact, soggy mat with few interstices; and 4) litter which had never been covered with water and which contained many interstices.

An expanded line intercept (50 m long) of the forest floor in each section was used to obtain a quantitative estimate of the relative area occupied by these forest floor types. In April the southern part contained very little open water and most of the area was above water level whereas the northern part contained much open water and many ponds choked with leaves, but relatively few emergent sites (Fig. 1). By late May the amount of water in both places was much reduced.

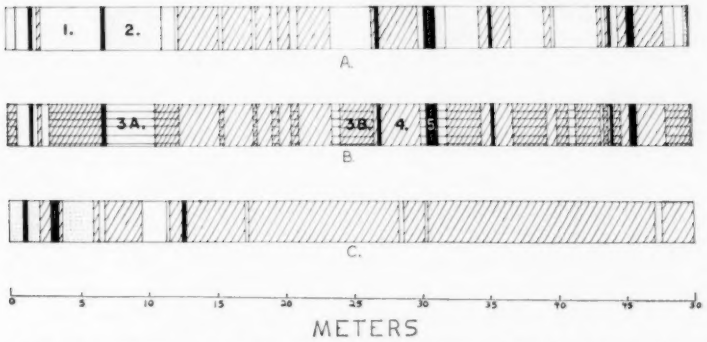


Fig. 1.—Expanded line-intercepts of the forest floor in the hardwood swamp. A. Northern section, April 20, 1958. B. Same line-intercept on May 29, 1958. C. Southern section, April 23, 1958. 1. Standing water. 2. Standing water choked with partly floating leaves. 3a. Previously submerged litter (dry). 3b. Previously submerged litter (wet). 4. Litter which had never been submerged. 5. Moss.

Weather data were recorded by three rain gauges and a Frieze constantly-recording Hygrothermograph in each of the sections except the middle one. In the northern section, the daily temperature maximum in late September was usually between 15° and 20° C; the minimum about 5° C. By mid-October maxima had fallen to approximately 13° - 15° C with minima still about 5° C. In late October temperatures were further lowered to 10° and 3° C for maxima and minima, respectively. The spring daily maxima were usually between 20° and 25° C; minima commonly between 0° and 10° C. The patterns of fluctuation in the northern and southern sections were similar although the latter usually had slightly higher air temperatures.

Relative humidities in October were 80 per cent or above much of the time and dropped as low as 40 per cent only during the afternoon, if at all. Virtually the same pattern was present in the spring except that high humidities were less frequent during the day. Night relative humidities were generally between 80 and 90 per cent in late April and early May. In late May the air was completely saturated at night.

There was no significant difference between the northern and southern sections in amount of rainfall reaching the forest floor.

A more detailed account of weather conditions is given by Heatwole (1959).

NATURE OF THE POPULATION STUDIED

A sample of 61 frogs was captured in the northern part of the swamp during the spring of 1957 to ascertain population structure. The range in body length was 26 to 44 mm, the latter concurring with size of adults in the same region given by Martof and Humphries

(*op. cit.*). There were two size groups, (1) young of the previous season (less than 34 mm s-v) and (2) juveniles more than one year old and adults. In the latter group, frogs of different year-classes could not be distinguished because of overlap in size between individuals of different ages. Fifty-nine per cent of the total population was in the first-year group indicating a heavy mortality before the second year.

LOCAL DISTRIBUTION AND HABITAT SELECTION

Field work was always initiated one week after cessation of breeding so that the local distributional pattern would not be obscured by the aggregation of mature individuals at breeding ponds.

An intensive search was made of all habitat types in the area. No wood frogs were in open areas such as pastures or fields and large populations occurred only in the hardwood swamp. One frog was at the edge of a bog mat, several were around ponds in oak-hickory forest and one was in a conifer swamp. However, in Minnesota, Bellis (1957) found large populations inhabiting a spruce-tamarack bog, and farther north conifer forest is commonly occupied by this species. Two possible explanations are (1) that there is geographic variation in habitat selection or (2) that wood frogs will inhabit conifer habitats only if hardwood swamp is not available. The first hypothesis has merit as Martof and Humphries (*op. cit.*) found morphological differences between Michigan populations and those farther east or west. Differences in habitat preference might parallel such structural differences. However, northern populations which are morphologically similar to Michigan ones inhabit conifer forest. More data are needed to decide between these two hypotheses.

Ecotonal areas between hardwood swamp and open areas received special attention. Only 33 wood frogs were found in the swamp-marsh ecotone; all but one were beneath the shade of trees at the swamp's edge. The single exception was in the open marsh approximately 50 feet from the nearest shade. Two individuals were found in the ecotone between marsh and oak-hickory; both were under trees. Thus it appears that one factor involved in habitat selection by *R. sylvatica* is the presence of arborescent vegetation. This probably has a greater influence than type of substrate or low vegetation as both of the latter were essentially marsh-like in the ecotones.

Abundance of wood frogs in the three sections of the swamp was compared by walking through each section and counting the number of frogs seen. Population density was higher in the northern section, with lesser numbers in the southern one and an intermediate number in the middle section (Table I). Frogs were not completely absent from the southern section as Table I suggests as a few individuals were found there on other occasions. For any given day, data in Table I are comparable between sections because sampling of the three parts occurred within several minutes of each other. Different days should not be compared as sampling was done at different times each day.

TABLE I.—Mean number of frogs observed per minute (amount of time spent in each section was usually about 15 minutes)

Date (1958)	Northern section	Middle section	Southern section
April 30	3.1	—	0
May 4	0.7	—	0
May 9	2.5	0.9	0
May 11	5.4	0	0
May 13	5.7	—	0
May 15	—	0.4	0
May 17	6.3	0.6	0
May 25	2.7	0	0
May 27	1.3	0.1	0
May 31	—	3.0	0

The litter was removed from a 6 m by 10 m plot in the southern section and from two of the same size in oak-hickory forest. Frogs were absent from all of them indicating that the low population densities observed in these areas were real rather than simply resulting from greater difficulty in finding frogs there than in other places. A permanent plot of the same size in the northern section yielded 5-35 frogs per observation period.

The northern section had a greater number of ponds than other wooded places and I believe this to be the factor responsible for its higher population density. Supporting evidence was obtained from studies on the permanent plot mentioned above. Frogs within it were periodically watched through binoculars from a platform built in a tree adjoining the site. Their locations were plotted on a map at the end of each observation period after all had been engaged in their normal activity for at least an hour and no longer gave evidence of being disturbed by my presence. Some frogs were probably overlooked or were hidden as the number counted varied from day to day. With the exception of 6 observations, all frogs were always within 15 cm of the pond's edge on either wet, compact litter or emergent sticks (Fig. 2). As the ponds dried up, they followed the receding water-line and maintained their locations at the water's edge.

The orientation of 79 per cent of frogs captured or observed during the study was toward the water; sixteen per cent faced away from it and 5 per cent were parallel to the shore.

In order to determine the interaction of substrate moisture and litter structure in influencing habitat selection, the following experiment was performed. Two boxes (90 cm x 60 cm x 17 cm) were filled to a depth of 3.5 cm with muck taken from the northern section. In one-half of each box the muck was left bare. In one of the boxes, half of the area was covered with a 3 cm layer of litter from the northern section. The other box had half of the surface covered with small pieces of bark lying loosely on the soil. Both boxes were covered with plate glass except for an opening 5-10 cm wide at each end. These were covered with screen. The boxes were placed in a window-

less room where temperatures ranged from 15° to 20° C and relative humidities from 22 to 54 per cent. Lights were kept on continually. A series of 6 frogs from the northern section was used. A rotation system was employed in which a given frog was kept in the experimental box 48 hours, after which it was replaced by another animal.

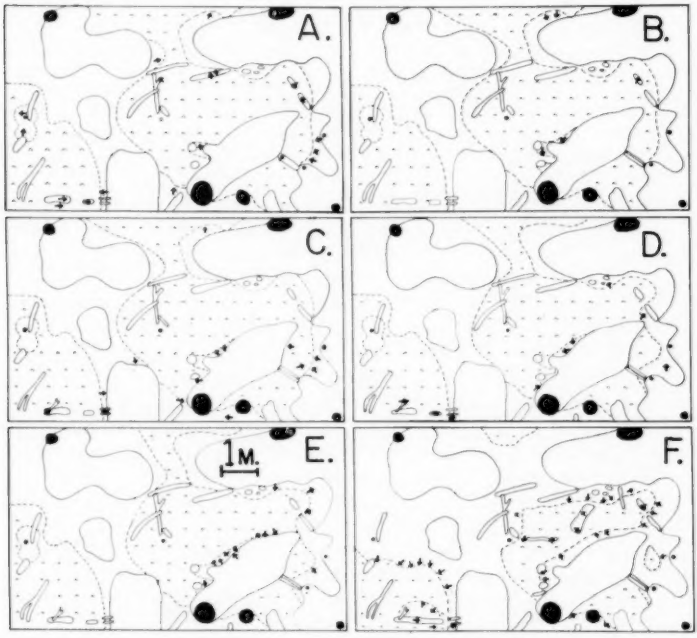


Fig. 2.—Position of wood frogs on a 6 m by 10 m plot in the northern section of the hardwood swamp. A. April 22, B. April 27, C. April 29, D. May 4, E. May 6, F. May 10. Elevated areas and sticks outlined with solid lines; compact litter with dotted line. Open water represented by small v shaped marks. Shaded areas represent bases of trees. Arrows represent frogs and point in the direction the animals were facing. Elevated areas contained litter which had never been submerged.

The experimental periods were divided in two parts; an initial period of 23-34 days during which the substrate was kept continually wet. This was followed by a period in which materials in the boxes were no longer watered and drying was allowed to continue for 20 days. The results from the second period were separated into sub-periods of 10 days each for comparison between different levels of substrate moisture. In the box containing leaves, the experiment was repeated for the wet and the first dry period and the results of the duplicate

runs grouped together. In the box with bark the first and second dry periods were repeated. In both instances the results of duplicate runs were similar.

During the wet period (114 observations) frogs were always on the surface of the substrate in both boxes. In the early sub-period of the drying stage (80 observations) frogs were found on the surface in 91 per cent of the observations and under bark or leaves 9 per cent. With further drying of the substrate (34 observations) the percentage of observations in which they were under cover increased to 29 (71% on surface). Thus, reduced substrate moisture influenced microhabitat selection by stimulating the frogs to seek cover where more moist conditions prevailed. When substrate moisture was continually high a decided preference was shown for bare humus rather than leaves. In the wet period, 81.6 per cent of the observations were of frogs on the humus side of the container and 18.4 per cent of frogs on leaves. It appears that *R. sylvatica* responds to the structure of the substrate and inhabits a flat surface unless adverse moisture conditions force it to seek cover.

The litter was removed from an 8 square meter plot on each of three days (Oct. 6, 13, and 18). The ponds had dried up and on October 6 places which had been pond bottoms were now areas of exposed, decayed leaves. Abscission was just beginning. Frogs were absent from the former pond-bottoms and were now under leaf-litter on elevated sites. This situation did not change even after abscission had been completed and all areas were covered with a carpet of leaves (Table II). Apparently by the time newly-fallen leaves were abundant

TABLE II.—Number of frogs per square meter in excavated plots in the northern part of the hardwood swamp

	Oct. 6	Oct. 13	Oct. 18
Elevated area with cover	0.75	0.50	0.13
Dry pond-bottom without cover	0	0	0
Air temperature at noon (°C)	17.5	15.5	6.0

enough to provide shelter in the dry pond-bottoms, temperatures were low and the frogs too sluggish to make any large-scale return. On October 6 (temperature 17.5° C) five of the six frogs hopped from under the litter as I was excavating near them. On October 13 (15.5° C), the frogs were all inactive and did not move even when the leaves were removed from above them. On October 18 (6° C) a single sluggish frog was found beneath the litter on muck. Temperatures given here are noon air temperatures. Hence they were near the maximum for the day and the frogs' activity probably at its daily peak when the plots were excavated.

The decrease in number of frogs in the plots during October may perhaps be associated with movement into the muck for overwintering as Wright (1914) gave October 30 as the latest date that wood frogs were seen in an 8-year study at Ithaca, N.Y. In southern Michigan,

Blanchard (1933) reported *R. sylvatica* under leaves on November 9, associated with other amphibians in what he considered overwintering groups.

ACTIVITY

The activity of poikilotherms is governed to a large extent by body temperature and hence by environmental temperatures. Within the range of field conditions in the spring, more frogs were observed at higher temperatures than at lower ones (Fig. 3). The same was true for relative humidity (Fig. 4). However, the higher temperatures were often accompanied by low humidities and vice versa. Hence each factor tended to modify the effect of the other and a broad scatter of points resulted on Figures 3 and 4.

Two groups of frogs were periodically observed during a 24-hour period (May 17-18, 1958). The first group consisted of those in the swamp and was sampled by counting the number of frogs observed in the range of lantern light (or an equal distance in daylight) on either side of a predetermined path 25 m long. The second group was made up of individuals on an elevated, open area adjacent to the swamp. This site was characterized by an abundance of *Impatiens capensis* 10-15 cm high. During the night a Coleman lantern hung from a tree limb about 1.5 m above the ground at one edge of the clearing and provided faint illumination. At hourly intervals I walked across the clearing and counted the number of frogs seen.

During the night few frogs were seen in the swamp but at sunrise the number increased sharply even though temperature did not

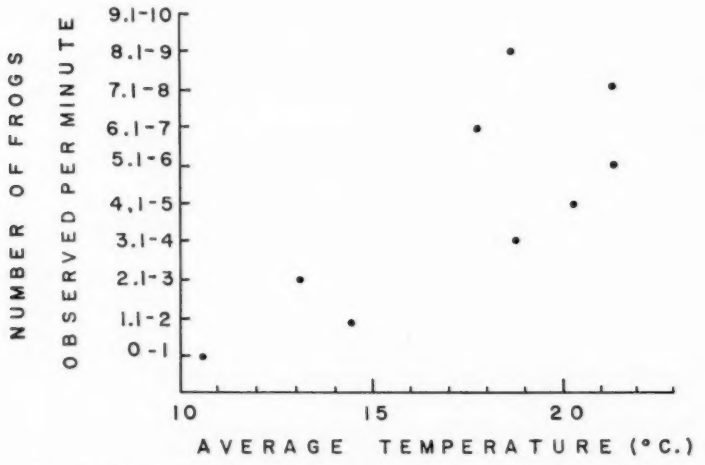


Fig. 3.—Air temperature and activity of wood frogs in the northern section of the hardwood swamp.

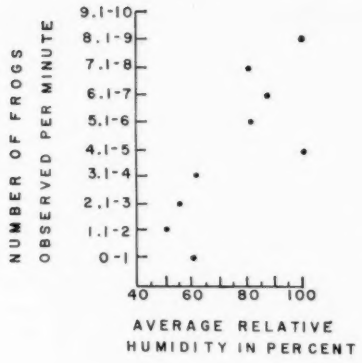


Fig. 4.—Relative humidity and activity of wood frogs in the northern section of hardwood swamp.

increase until two hours later (Fig. 5). Frogs first appeared in the clearing during an overcast period of late afternoon, i.e., when both temperature and relative humidity were high. They were there during the night in fluctuating numbers, perhaps because of the light of the lantern, and remained through the morning which was rainy and overcast. After the sky cleared, the frogs returned to the swamp where there were trees overhead.

Frogs in the permanent plot were watched with binoculars from a platform in a tree to observe habitat utilization under natural conditions. Observation periods varied from 1 hour and 20 minutes to 3 hours and 25 minutes. During these periods 11-46 per cent of the frogs did not change location and even during the longest one, 21 per cent remained in the same spot the entire time. These are probably overestimates of wood frog movements as 9-43 per cent changed location when I disturbed them in entering the area and their return to the original sites constituted the only movement recorded for many of them during the entire period (Table III).

The chief factor stimulating activity of undisturbed frogs was the movement of an invertebrate in front of them although feeding did not always occur at such times. Sometimes the frogs only turned their heads or leaned forward.

Excluding movements of animals returning to their original locations after having been disturbed when I entered the area, distances covered were slight. Three frogs moved approximately 1.5 m during an observation period and 7 moved about 0.5 m. All other activity consisted of feeding, moving an appendage, turning around without changing location, or hopping short distances (25 cm or less). It appears that the "activity period" of wood frogs is characterized by their sitting motionless unless some prey item comes within range or they are disturbed. Occasionally an individual would move in response to movement of another frog.

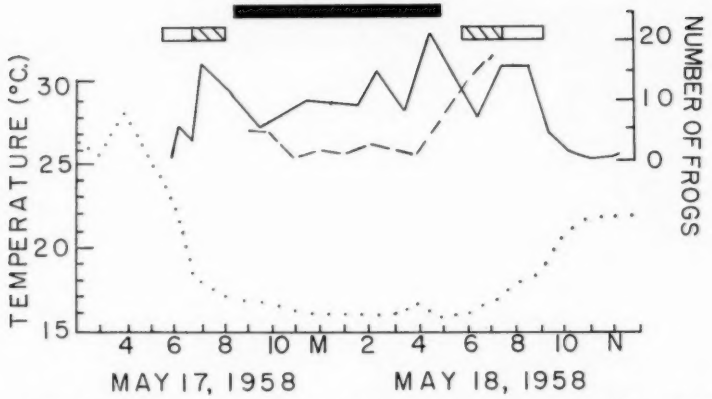


Fig. 5.—Weather conditions and activity of wood frogs on May 17-18, 1958. Solid bar indicates period of darkness; open bar indicates overcast periods and cross-hatched bar indicates rain. Solid line represents number of frogs in clearing at the edge of the swamp. Broken line represents number of frogs along a transect through swamp. Dotted line represents air temperature 3 cm above the ground. M signifies midnight; N signifies noon.

Inactive frogs probably spend their time in submerged litter at the bottom of ponds as several were observed in such situations for long periods. This may account for the variable number found in the permanent plot on different days.

During the springs of 1957 and 1958, the escape pattern of wood frogs was recorded 1,013 times. In 47.8 per cent of the observations the frogs dived into a pond, swam under water for a distance varying from 15 cm to 1.5 m, and then came to the surface where they floated with their heads out of water. The second largest number of escapes (39.4%) followed a similar pattern which ended in the frog hiding in loose, submerged litter in the bottom of the pond instead of surfacing. All other escape behavior involved (1) hopping over emergent litter or muck (11.4%), (2) entering cavities under the bases of trees (0.7%), (3) going beneath logs or sticks on land (0.5%), and (4) diving into ponds and lying on the bottom but not concealed in submerged litter (0.2%).

As most of the frogs faced the water I thought the preponderance of escapes to aquatic situations might simply be the result of their hopping in the direction they happened to be facing when disturbed. To test this hypothesis the escape behavior of 61 frogs was recorded both before and after their capture. When released at their original location but facing parallel to the shore instead of toward the water, the proportion of attempted escapes to non-aquatic situations did not change significantly (Fig. 6). Therefore the direction in which the

frogs faced was not the prime factor determining whether they would enter the water or not. Similarly, handling the frogs did not affect whether they would attempt escape into the water or onto land. However, of those hopping into the water, the percentage of escapes to submerged litter decreased by almost one-half after capture. There was a corresponding increase in the proportion which surfaced. At the time of release the frogs had doubled the exertion put forth during the initial attempt to escape. The consequent increase in oxygen demand may explain the change in behavior.

Escape behavior was not studied in detail after the ponds had dried up. However, casual observation indicated that the most common pattern then was hopping over litter rather than seeking cover beneath it.

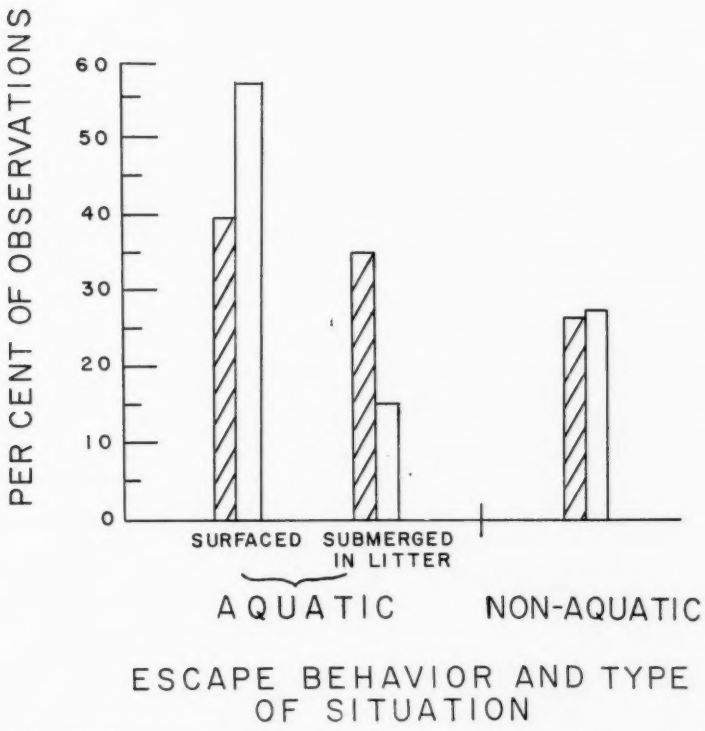


Fig. 6.—Per cent of frogs attempting escape to aquatic and non-aquatic situations. Open bar represents observations of escape behavior before capture; cross-hatched ones escape behavior after capture and release.

TABLE III.—Per cent of frogs displaying activity of various types during observation of the permanent plot in the northern part of the hardwood swamp, 1958 (total for a given period exceeds 100 per cent when some frogs were engaged in several types of activity; numbers of frogs per period ranged from five to thirty-five)

	Apr. 22	Apr. 27	Apr. 29	May 4	May 6	May 10
No change of position or location	21	20	14	11	38	46
Feeding	0	0	0	0	23	3
Alerted but did not feed	16	20	0	0	0	3
Response to movement of other frogs	0	0	0	0	8	0
Reason for change of position or location unknown	42	40	43	67	23	40
Return to original location after disturbance when I entered the plot	21	20	43	22	15	9

DISCUSSION

It is obvious that even in a particular locality no one environmental factor is solely involved in habitat selection. Furthermore, the effect of each specific factor is modified by the action of others and consequently something which is important at one time may become relatively insignificant as seasonal changes in the whole environmental complex take place.

R. sylvatica inhabits forests. Individuals were found in an ecotone between marsh and swamp, but with the exception of one frog, none were found beyond the shade of trees. In the ecotone itself, conditions other than presence of shade were essentially marsh-like. Frogs were active in a clearing on a heavily overcast morning but returned to the adjacent swamp when the sky cleared. The few non-forested habitats from which *R. sylvatica* has been recorded are shaded. For example Black (1938) and Barr (1953) report it from the twilight zone of caves. All of these observations combine to indicate that shade must influence habitat selection of this species. Shady places are characterized by reduced light intensities and temperatures and relatively high humidities. The same is true of overcast periods. Thus, one of these (or a combination of several) are probably directly involved. Not enough data are available to ascertain which one or ones are most important.

Within forested areas, the presence of ponds appears to be the chief environmental feature to which *R. sylvatica* responds. Individuals sit on flat, previously submerged litter at the edges of the ponds and follow the water-line as it gradually retreats during the season. They seem to be reacting to several features associated with ponds. (1) The structure of the newly emerged substrate seems to

be important as under experimental conditions a flat substrate similar to that immediately surrounding the ponds was occupied rather than equally wet leaf-litter. (2) The amount of substrate moisture is involved as caged animals left a flat substrate when it became too dry and sought cover under leaves. (3) The presence of the pond itself governs the orientation of frogs; they tend to face open water rather than the bank.

In the past, frequent observation of wood frogs routed from forest floor litter has led to an exaggerated view of their terrestrial tendencies. The litter is not the preferred habitat but is occupied after drying of more suitable sites around woodland ponds. In some forest types such as oak-hickory, where ponds are frequently small and commonly dry up early in the season, wood frogs might be found in leaf-litter throughout most of the summer.

These remarks do not necessarily apply to this species during the breeding season as other factors are undoubtedly operating then. I have observed breeding aggregations of *R. sylvatica* in ponds as far as one-fourth mile from the nearest forest.

REFERENCES

BARR, T. C. JR. 1953. Notes on the occurrence of ranid frogs in caves. *Copeia,* **1953**:60-61.

BELLIS, E. D. 1957. An ecological study of the wood frog, *Rana sylvatica* Le Conte. Ph.D. Thesis. Univ. of Minnesota (L.C. Card No. Mic 58-1105) 169 p. Univ. Microfilms. Ann Arbor, Mich. (*Dissertation Abstr.*, **18**(1958):1537).

BLACK, J. D. 1938. Additional records of *Rana sylvatica* in Arkansas. *Copeia,* **1938**:48-49.

BLANCHARD, F. N. 1933. Late autumn collections and hibernating situations of the salamander *Hemidactylium scutatum* (Schlegel) in southern Michigan. *Copeia,* **1933**:216.

GETZ, L. L. 1961. Factors influencing the local distribution of *Microtus* and *Synaptomys* in Southern Michigan. *Ecology,* **42**:110-119.

HEATWOLE, H. 1959. The forest floor and its utilization by selected species of terrestrial amphibians. Ph.D. Thesis. Univ. of Michigan (L.C. Card No. Mic 60-2537) 425 p. Univ. Microfilms. Ann Arbor, Mich. (*Dissertation Abstr.*, **21**(1960):380).

——— AND L. L. GETZ. 1960. Studies on the amphibians and reptiles of Mud Lake Bog in southern Michigan. *The Jack Pine Warbler,* **38**: 107-112.

MARTOF, B. S. AND R. L. HUMPHRIES. 1959. Geographic variation in the wood frog, *Rana sylvatica. Am. Midl. Nat.,* **61**:350-389.

VEATCH, J. O., L. C. WHEETING AND A. BAUER. 1930. Soil survey Washtenaw County, Michigan. U. S. Dept. Agr. Bureau Chemistry and Soils. Ser. 1930, No. 21.

WRIGHT, A. H. 1914. North American anura: life histories of the anura of Ithaca, New York. Carnegie Instit. Wash. Publ., 197.

The Site of Udonella caligorum (Trematoda) upon Parasitic Copepod Hosts

DAVID CAUSEY
University of Arkansas and Gulf Coast Research Laboratory

ABSTRACT: The literature indicates that *Udonella caligorum* tends to select the egg strings of the host copepod as a site of attachment in European waters, and the body of the copepod in American waters. Data for two species of parasitic copepods from American waters, having this trematode upon them, confirms the apparent choice of the body of the copepod as a site.

Udonella caligorum Johnston, 1835 is a small leech-like parasitic trematode which apparently spends its entire life upon various species of parasitic copepods of marine fish. It has been reported from European waters (Dawes, 1946); the Atlantic Coast of the U.S. and Canada (Dawes, 1946; Price, 1938; Tortugas (Price, 1938) and Port Aransas, Texas (Causey, 1956) in the Gulf of Mexico; and Monterey Bay, California, (Guberlet, 1936). I add two new records, Ocean Springs, Miss., and Georgetown, British Guiana.

Most of the fish hosts and the parasitic copepods mentioned in the literature are cited (Table I). The fish listed are all marine, and include both cold water and warm water types, ranging widely over the class. Three suborders (following Wilson, 1932) of parasitic copepods are included: the Cyclopoida, Caligoida, and Lernaeopodoida. Free swimming caligids are often caught in the tow, and apparently, according to Dawes' record, the trematodes go with them. Price's careful survey and Dawes' tabulation make it evident that probably only one species of trematode is involved. To one interested in host specificity, ecological relations, and distribution, this association of so many kinds of fish and parasitic copepods, and a single species of trematode is surprising, if not improbable!

With sufficient specimens of infested copepods, one can find all stages of the life cycle of the trematode from the stalked egg to the mature worm. Price states, "The life history of this species, so far as represented in the available material, is essentially the same as that given by van Beneden (1858). Van Beneden gives more stages (less clearly) than Price; Dawes copies Price's figures. The one point in the life cycle which is not evident is the transfer from copepod to copepod. Van Beneden thought the change took place during the free swimming stage of the copepod. That this could occur, unless the transfer took place during coitus of the copepods, seems unlikely. All example of coitus I have found thus far, admittedly few, were taken from the fish surface and not from the plankton. One can consider the possibility, on the basis of free swimming copepods carrying the trematodes, that the transfer occurs after the copepods have settled on the fish. I suspect that this occurs slowly, as I have several

TABLE I.—Fish and copepods associated with *Udonella*

Fish	Copepod	Source
Pleuronectus hippoglossus	Caliges	Van Beneden, 1858
Gadus morrhua	Caliges	Van Beneden, 1858
Trigla gurnardus	Calige	Van Beneden, 1858
Neomaenis griseus	"*Argulus* sp."	Price, 1938
Gadus callarias	*Caligus* sp.	Price, 1938
Myliobatis californicus	*Trebius latiturcatus*	Price, 1938
Halibut, cod, pollack, wolf-fish, common ling, hake, and flounder	*Caligus* spp.	Dawes, 1946
Free swimming	*C. rapax* and *C. curtus*	Dawes, 1946
Cod	*Anchorella uncinata*	Dawes, 1946
Carcharias milberti	*Alebion carchariae*	Dawes, 1946
Amphipholis sp.	*Cancerilla vulgaris*	Dawes, 1946
Neomaenis griseus	*Argulus* sp.	Dawes, 1946
Zygaena malleus	*Alebion carchariae*	Dawes, 1946
Wolf-fish	*Caligus minutus*	Dawes, 1946
Shadowfish	*Anchorella* sp.	Dawes, 1946
Ballan wrasse	*Caligus labracis*	
(Plus other continental hosts).	*C. centrodonti*	
Pogonias cromis	*Caligus haemulonis*	Causey, 1956
Galeichthys felis	*Lepeophtheirus bonaci*	
Pristis pectinatus	*Alebion carchariae*	

pairs in coitus, with only one of the couple in each case having attached trematodes.

There is a marked difference in opinion between European writers, e.g., Van Benden and Dawes, and American observers, e.g., Price and the present writer, as to where the trematodes are found on the copepods. Van Benden says, "Il habite le corps de plusieurs espèces de caliges, surtout les tubes ovifères des femelles," and his fig. 1 of plate I shows a number of the trematodes attached to an egg string. Dawes states, "Mainly on the egg sacs of female copepod." Price says, "Body and appendages of copepod." It is not customary in technical writing on Crustacea to refer to the egg strings as appendages, and I assume Price means the true, jointed appendages.

Besides a few specimens of *Caligus haemulonis* with trematodes attached to the carapace which came from a drum examined at Port Arkansas, Texas, I have two extensive collections: *Alebion carchariae* Kroyer, 1863 which was taken from *Pristis pectoralis* off Georgetown, British Guiana, by Mr. Harvey B. Bullis, Jr., and *Lepeophtheirus bonaci* Pearse, 1953, which was taken off *Galeichthys felis* at Ocean Springs, Miss., by Mr. J. Y. Christmas. Both collections have a number of the trematodes attached to the copepods, and are the basis of the present paper. The distribution of the trematodes over the bodies of the respective copepods is indicated in Tables II and III.

TABLE II.—Location of *Udonella caligorum* on *Alebion carchariae* from Georgetown, British Guiana

Copepod females with egg strings	2		
Copepod females without egg strings	19	Total number of females	21
Trematodes on carapace	13	Trematode eggs on carapace	0
Trematodes on genital segment	0	Trematode eggs on genital segment	0
Trematodes on egg strings	0	Trematode eggs on egg string	0
		Total number of males	5
Trematodes on carapace	3	Trematode eggs on carapace	0
Trematodes on genital segment	0	Trematode eggs on genital segment	0

There was a total of 44 trematodes on 26 specimens of *Alebion carchariae*. The largest number of trematodes on a particular copepod specimen was 10. As indicated by the Table, all the trematodes were on the carapace, usually attached to either or both borders. (Fig. 1.) No eggs were present. This suggests that it was either too early or too late, probably the former, as most of the trematodes were mature. There were a few very small ones present. The figures indicate that the female is more likely to be parasitized than the male. In addition to the tabulation, the collection included 4 mutilated specimens of copepods, only the carapace being present, with trematodes on 3 of them. No attempt was made to determine the sex of these specimens. There were also 7 loose trematodes in the vial. The latter and the trematodes on the mutilated specimens are not included in the tabulation.

TABLE III.—Location of *Udonella caligorum* on *Lepeophtheirus bonaci* from Ocean Springs, Mississippi

Copepod females with egg strings	20		
Copepod females without egg strings	3	Total number of females	23
Trematodes on carapace	5	Trematode eggs on carapace	3
Trematodes on genital segment	6	Trematode eggs on genital segment	15
Trematodes on egg strings	3	Trematode eggs on egg strings	2
		Total number of males	8
Trematodes on carapace	0	Trematode eggs on carapace	0
Trematodes on genital segment	1	Trematode eggs on genital segment	2

There was a total of 15 trematodes on 31 specimens of *Lepeophtheirus bonaci*. The largest number of trematodes on a particular copepod specimen was 2. Here again the tabulation indicates that the female is the more likely to be parasitized, and with this species

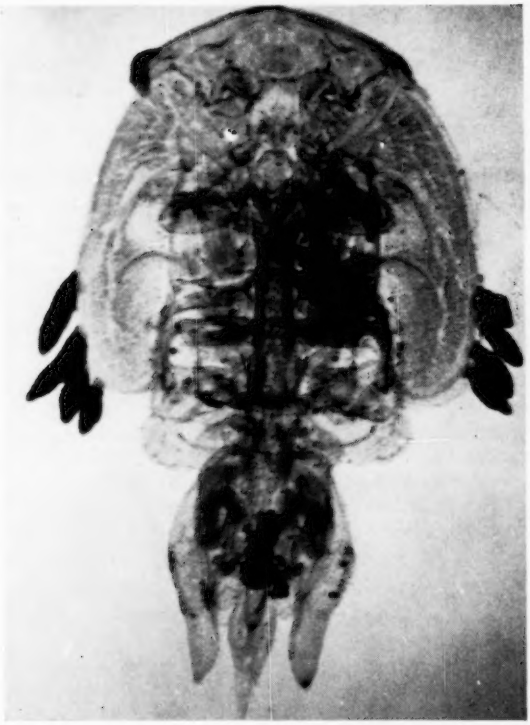


Fig. 1.—*Alebion carchariae* showing 9 specimens of *Udonella caligorum* attached to carapace. Photomicrograph of mounted specimen.

of copepod the genital segment is preferred as a site of attachment. Trematode eggs were present, an occasional egg being attached almost anywhere, but in several examples the eggs attached to the genital segment formed a cluster so large as to almost hide this portion of the copepod body. It will be noted that in this species of copepod trematodes and trematode eggs were found attached to the egg strings. It is evident, however, that in both species of copepod some part of the body is most likely to be selected as a site.

With all due allowance for the uncertainty of what collections received in the mail may actually represent, the literature on this host-parasite relationship indicates a descrepancy. Apparently the stages of *Udonella* occur more often on the egg strings of the host copepod in European waters and on the carapace and genital segment of the host copepod in American waters.

REFERENCES

CAUSEY, D. 1956. Ad Infinitum. *Ed. Focus*, **27**(1):13-15.

DAWES, B. 1946. The Trematoda. Cambridge, 644 p.

PRICE, E. W. 1938. North American monogenetic trematodes. *J. Wash. Acad. Sci.*, **28**(1):183-198.

VAN BENEDEN, P. J. 1858. Mémoire sur les vers intestinaux. Suppl. *C. R. Acad. Sci., Paris*, 2, 376 p.

WILSON, C. B. 1932. The copepods of the Woods Hole Region, Massachusetts. *Bull. U.S. Nat. Mus.*, **158**, 635 p.

The Genus Naematelia[1]

ROBERT J. BANDONI
Department of Biology and Botany, University of British Columbia, Vancouver 8

ABSTRACT: Observations were made on cultures of *Tremella encephala* and on herbarium and field collections of this species. Repeated isolations from the fleshy core and from basidiospores demonstrate that the basidiocarps are composed of two discordant elements. The name *Naematelia*, originally based on this species, is then a *nomen confusum*. The present status of other species is discussed and descriptions and illustrations are given for several species.

In 1816[2], Fries established the genus *Naematelia* in which he included the single species, *N. encephala* (Pers.) Fries. In this species, the basidiocarps consist of a firm, fleshy core surrounded by a gelatinous hymenial layer, while in other species of *Tremella*, in which genus it had originally been placed, basidiocarps are gelatinous throughout. In his Systema, Fries (1822) included two additional species, *N. rubiformis* Fries and *N. nucleata* (Schw.) Fries. Approximately twenty species have been described since that time.

Lloyd (1922) divided the genus into two sections: 1, *Encephala*, including only *N. encephala*, and 2, *Naematelia*, in which he placed *N. nucleata* and *N. globulus* Corda. He discussed thirteen species in addition to the above, but included all under "Other 'Species.'" Lloyd believed that the two sections constituted separate genera, though he did not describe them as such. He also stated that "Tulasne and Brefeld both finding the basidia of *Naematelia* the same as those of *Tremella*, disregarded the heterogeneous structure of the tissue and included the genus in *Tremella*." Others, including Patouillard (1900), Rea (1922), Bourdot and Galzin (1928), Neuhoff (1936), and Martin (1944 and 1952) have followed a similar course, but

[1] I wish to express my appreciation to C. R. Benjamin and J. A. Stevenson, Plant Industry Station, Beltsville; Prof. J. N. Couch, University of North Carolina, Chapel Hill; Prof. R. Heim, Muséum National d'Histoire Naturelle, Paris; Prof. G. W. Martin, State University of Iowa, Iowa City; Stanley Jay Smith, New York State Museum, Albany; and to the Director, Royal Botanic Gardens, Kew; for the loan of specimens used in this study. The research was supported in part by grants from the National Research Council of Canada and the President's Research Committee of the University of British Columbia.

[2] Fries (1822) cites *Naematelia* Fries as published in Liljebl. Sv. Fl. (1815). This is evidently a reference to the third edition of Liljeblad's Svensk Flora, which I have not seen. According to Pritzel, the third edition of this work was published in 1816.

without giving reasons for doing so. Coker (1920), Burt (1921) and Kobayasi (1939) recognized *Naematelia* as a separate genus in their treatments of the Tremellaceae, although only Coker included forms with calcareous "nuclei" such as *N. nucleata.*

A study of *N. encephala* was undertaken in order to clarify its taxonomic position and to learn more concerning its structure. Observations were made on field collections, herbarium specimens and cultures of this and related species. A summary of the taxonomic status of a number of the species is included at the end of this paper.

N. encephala occurs most commonly on coniferous wood such as that of *Pinus, Abies, Larix* and *Pseudotsuga.* Observations on collections made in British Columbia reveal that this species is usually associated with *Stereum sanguineolentum* (Alb. & Schw. ex Fr.) Fries. In three, of approximately twenty collections made, basidiocarps of the *Naematelia* appeared to arise directly from those of the *Stereum,* rather than from the underlying substrate. Herbarium specimens of this species and of *Tremella tremelloides* (Berk.) Massee (= *Naematelia aurantia,* sensu Burt, 1921) were found to have species of *Stereum* present in many cases. The possibility that the fleshy portion of the *Naematelia* basidiocarps actually belongs to the *Stereum* became apparent. This possibility was strengthened by the fact that a number of species of *Tremella* occur only on the fructifications of other fungi.

Cultures of *N. encephala* were obtained by suspending portions of the hymenia of sporulating basidiocarps over malt agar. Basidiospores landing on the agar germinated by the production of several blastospores (Fig. 1 a). Budding of the latter occurred (Fig. 1 b) and large yeast-like colonies were produced. Transfer of these to other standard media such as malt extract, oat, yeast extract and corn meal agar failed to induce hyphal formation, although the fungus was easily maintained in this yeast-like form and on these media.

Attempts were made to obtain cultures from freshly collected specimens through direct transfer of bits of the basidiocarps. These were removed as aseptically as possible from both the gelatinous and fleshy portions of the fructification and placed directly on media of the types previously mentioned. No cultures were obtained from the gelatinous areas, but the fleshy cores produced rapidly growing cultures in each attempt. Since the hyphae of these cultures did not resemble those of the gelatinous portion of the *Naematelia,* they were compared with cultures obtained through seeding of spores of *Stereum sanguineolentum* on malt agar. The two appeared to be identical. If both the core and the gelatinous portions belonged to a single fungus, one would expect to obtain identical cultures from the two regions and with equal ease.

Malt agar plates were then inoculated with both the yeast-like phase of the *Naematelia* and hyphal cultures of the *Stereum.* Germination of the cells of the former by germ tube (Fig. 1 c) occurred

within a few hours. Haustoria[3] (Fig. 1 e) were produced on the hyphae of *N. encephala* soon after dikaryotization and hyphae formed in this manner were identical with those of the hymenial region of that species. At points of contact between the growing hyphae of the *Stereum* and the still yeast-like colonies of the *Naematelia*, compact masses of hyphae were sometimes formed. These appeared woolly externally, but were essentially like the core of the *Naematelia* internally. No basidia were produced, however, nor was a gelatinous layer formed.

It would seem probable that *N. encephala* is parasitic on this, and possibly other species of *Stereum*, though further study of this is necessary. The fact that the core of this species consistently yielded the same fungus, and that this was not the *Naematelia*, demonstrates that the duplex nature of the *N. encephala* fructifications is brought about by the presence of two distinct fungi. The name *Naematelia* is then to be considered a *nomen confusum*, since its characters were derived from two discordant elements. Those species with fleshy cores do not differ in other respects from species of *Tremella*, in which genus they should properly be placed. Those forms with calcareous nodules have been placed in *Exidia*, as noted below.

TAXONOMIC NOTES

All species are listed in alphabetic order. The abbreviations following collection data are those of various herbaria in which the specimens are deposited (J. Lanjouw and F. A. Stafleu, 1956). What is regarded as the correct name is indicated in bold-faced type.

Naematelia atrata Peck
See under *N. nucleata*.

Naematelia aurantia Burt
See under *Naematelia quercina*.

Naematelia cerebriformis Ellis ex Peck
See under *N. encephala*.

Naematelia cinnabarina Mont. Ann. Sci. Bot. III, 10: 120. 1848.
Tremella cinnabarina (Mont.) Pat. Essai Tax. 21. 1900.
Tremella samoensis Lloyd, Myc. Writ. 5: 875. 1919.

Portions of the types of *T. samoensis* and *N. cinnabarina* (both in Lloyd Collection BPI) were examined. There does not seem to

[3] These structures were first designated as haustoria by Olive (1946) in discussing a parasitic species of *Tremella*. In a previous paper dealing with that genus (1958) I suggested that, since the structures were to be found in a number of species considered to be saprobic, the use of the term haustorium would be incorrect. However, further study of this group has led me to believe that many of the species previously considered saprobic are actually parasitic on other fungi. The term is accepted here, although some may disagree with its use since the structures are unlike haustoria of fungi parasitizing higher plants.

be sufficient difference between the two to maintain them as separate species.

Naematelia corticola Berk. & Cooke, Linn. Soc. Bot. Jour. 15: 392. 1876.

The type specimen (K) was examined, but no tremellaceous fungus was found. There is a deuteromycete present on the material and the description may have referred to it.

Naematelia encephala (Pers.) Fries, Syst. Myc. 2: 227. 1822.
[*Tremella encephaliformis* Willd. Mag. für Bot. 2(4): 17. 1788].
[*Tremella encephala* Pers. Syn. Fung. 623. 1801 (cites Willd.)].
[*Naematelia encephala* [Pers.] Fries, Obs. Myc. 2: 370, 1818].
Tremella encephala Pers. Myc. Eur. 1: 98. 1822.
Tremella encephaloidea Spreng. Syst. Veg. 4(1): 534. 1827.
Naematelia cerebriformis Ellis ex Peck, N. Y. State Mus. Ann. Rep. 30: 49. 1878.
Tremella alabastrina Bref. Untersuch. 7: 129. 1888.
Naematelia japonica Lloyd, Myc. Writ. 4: L. 54, p. 5. 1915.
Tremella japonica (Lloyd) Yasuda, Bot. Mag. Tokyo 29: 385. 1915.
Naematelia encephaliformis [Willd.] Coker, Jour. Elisha Mitchell Soc. 35: 137. 1920.
Tremella rubiformis (Fries) Quél. sensu Bourdot & Galzin, Hymén. Fr. 25, 1928, fide Neuhoff.
Tremella encephaliformis Willd. ex Olive, Jour. Elisha Mitchell Soc. 62: 66. 1946.

The original and subsequent descriptions of this species were based upon two separate fungi. Therefore, it should be emended as follows:

Parasitic, the basidiocarp in the form of a continuous layer surrounding a fleshy erumpent core formed by the host, gelatinous, the surface minutely roughened to rugose or plicate, sometimes with thick flattened lobes, yellowish, drying pale yellow to cinnamon; hyphae 1.5-4μ in diam., with clamps and haustoria; hymenium amphigenous, the fertile layer extending from the surface to as much as 150μ below it; probasidia borne terminally or laterally, often in opposite pairs along the fertile hyphae, at first subglobose to cylindric or fusiform, mostly globose to subglobose or obovate at maturity, cruciate-septate, 13-20 $\times$ 13-17(-20)μ; epibasidia reaching 150 $\times$ 2-4μ, swollen to 6-7μ apically; basidiospores broadly oval or subglobose, (8-)9-11 $\times$ 7.5-9μ, germinating by repetition.

Type locality:—Europe.

Habitat:—Commonly adjacent to, or on fructifications of *Stereum* on conifer wood or, less frequently, on angiosperm wood.

Distribution:—Europe, Japan, North America.

Illustrations:—Brefeld, Untersuch. 7, pl. 3, ff. 20-24; Neuhoff, Pilze Mitteleur. 2, Col. pl. 3, ff. 1-12; Bourdot and Galzin, Hymén. Fr. f. 15.

Tremella encephala [Willd.] Bref. var. *steidleri* Bres., found on oak, was not considered by Lloyd (1922) or Olive (1946) to warrant varietal designation. However, Bourdot and Galzin (1928) elevated Bresadola's variety to specific rank and their illustration

(Fig. 12) suggests that their fungus may be distinct. The type of *N. cerebriformis* (NYS) grew on *Carpinus caroliniana* in association with a species of *Stereum* and does not seem to be distinct from *T. encephala.*

Naematelia encephaliformis [Willd.] Coker
See under *N. encephala,* above.

Naematelia fragiformis [Pers.] Lloyd (as McGinty), Myc. Writ. 7: 1150. 1922.
Tremella fragiformis Pers. Syn. Fung. 2: 622. 1801.
Dacrymyces fragiformis [Pers.] Fries, Syst. Myc. 2: 229. 1822.
Considerable doubt exists concerning this form and Kennedy (1958) lists it under excluded species in her treatment of *Dacrymyces.* Neuhoff (1936) considered it to be the same as *Tremella encephala.*

Naematelia frondosa (Fries) Bonorden, Handb. Myk. 152. 1851.
Tremella frondosa Fries, Syst. Myc. 2: 212. 1822.

Naematelia fuscobasis Lloyd ex Stevenson & Cash, Bull. Lloyd Lib. No. 35, Myc. ser. 8; 32. 1936.
Naematelia fuscobasis Lloyd, *nomen nudum,* Myc. Writ. 7: 1295. 1924.
The type specimen (BPI) does not seem to be a fungus. It consists of what appears to be a resinous exudate externally and is parenchyma-like internally. I could find no indication of fungus hyphae.

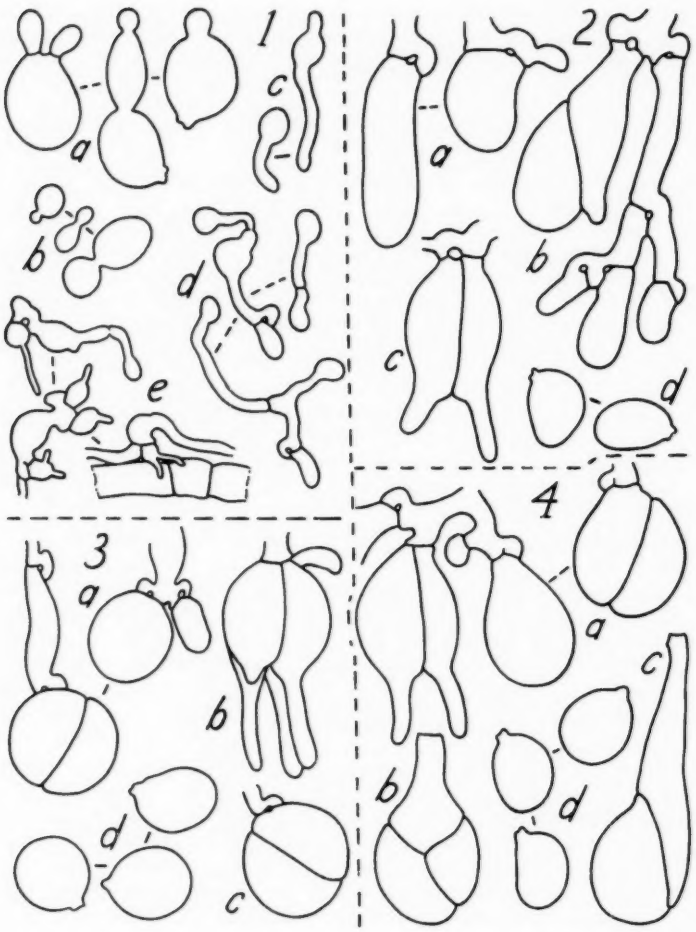
Naematelia gemmata (Lév.) Fries, Hym. Eur. 697. 1874.
Tremella gemmata Lév. in Demidoff, Voyage Russie Merid. 2: 95. 1842.
Exidia gemmata (Lév.) Bourd. & Maire, Bull. Soc. Myc. Fr. 36: 69. 1920.
This species has been considered by some (Rea, 1922, Bourdot and Galzin, 1928, and Donk, 1931) to be the same as *Exidia nucleata* Schw.) Burt. However, Neuhoff (1936) felt that it was distinct.

Naematelia globulus Corda, Ic. Fung. 1: 25. 1837.
Tremella globulus (Corda) Bref. Untersuch. 7: 126. 1888
Lloyd (1922) felt that this species is not the same as *Exidia nucleata* [Schw.] Burt, although the description which he gave certainly suggests that it is. As he pointed out, illustrations shown by Brefeld and Corda seem to be of two different species. That Lloyd himself was not certain as to the identity of this species is brought out by his statement (Myc. Writ. 7: 1166) that, "The genus [species], *Naematelia nucleata* (common in the States) and the same (or similar) species, *Naematelia globulus* (very rare in Europe) has never been collected before in a foreign country."

Naematelia guttaeformis Berk. & Br. Linn. Soc. Bot. Jour. 14: 77. 1875.

Tremella guttaeformis (Berk. & Br.) *comb. nov.*
Fig. 2

Fructifications hemispherical, gregarious, minutely roughened, 1-2 mm in diam. or becoming confluent and larger, gelatinous, borne on



Figs. 1-4.—All figures drawn with the aid of a camera lucida and reduced to approximately × 1000. 1. *Tremella encephala*. a, Basidiospores germinating by formation of blastospores. b, Yeast-like budding of cells. c, Germination of yeast-like cells by the formation of germ tubes. d, Fusion of germ tubes of compatible cells. e, Formation of haustoria, one shown attached to a hypha of *Stereum sanguineolentum*. 2. *Tremella guttaeformis*. a-c, Basidia and probasidia in various stages of development. d, Basidiospores. 3. *Tremella tremelloides*. a-c, Basidia and probasidia in various stages of development. d, Basidiospores. 4. *Tremella aurantia*. a-c, Typical basidia and probasidia showing variation in form. d, Basidiospores.

a thin, effused gelatinous layer, 1 cm or more in extent, luteus when soaked, drying horny, castaneous; in section, the hemispherical portions hollow, walls about 300-400μ thick; hyphae 2-5μ in diam., with numerous clamps and septa; hymenium forming an amphigenous surface layer; probasidia mostly clavate to subcylindric at first, becoming broadly clavate to elliptical, longitudinally to obliquely cruciate-septate, each with a conspicuous basal clamp through which proliferation occurs; epibasidia about 20-30 $\times$ 2-3μ; spores ovate, flattened adaxially, 8-12 $\times$ 5-7μ, germinating by repetition.

Type locality:—Ceylon.
Habitat:—On bark.
Distribution:—Known only from the type locality.

The type specimen (K) seems to be distinct from any described species of *Tremella*. It does not have a fleshy or calcareous core.

Naematelia japonica Lloyd
See under *N. encephala*.

Naematelia nucleata [Schw.] Fries, Syst. Myc. 2: 228. 1822.
[*Tremella nucleata* Schw. Naturf. Ges. Leipzig Schw. 1: 115. 1822].
Naematelia atrata Peck, N. Y. State Mus. Ann. Rep. 24: 83. 1872.
Exidia nucleata (Schw. ex Fries) Burt, Ann. Missouri Bot. Gard. 8: 371. 1921.
Exidia nucleata (Schw. ex Fries) Rea, Br. Bas. 735. 1922.

The type specimen of *N. atrata* (NYS) appears to be a young collection of *E. nucleata*. A specimen designated as the syntype (NYS) is also an *Exidia*, possibly *E. glandulosa* Fr.

Though this species is placed in *Exidia* at the present time, it is no more at home in that genus than in *Tremella*. The structure of its basidia indicates a close relationship with *Stypella, Protohydnum,* etc.

Naematelia quercina Coker, Jour. Elisha Mitchell Soc. 35: 135. 1920.
Sparassis tremelloides Berk. Grevillea 2: 6. 1873.
Tremella tremelloides (Berk.) Massee, Jour. Myc. 5: 184. 1889.
Naematelia aurantia sensu Burt. Ann. Missouri Bot. Gard. 8: 368. 1921. [*Tremella aurantia* Schw. in the sense of various authors, but not of Schweinitz].

Since *T. tremelloides* has long been confused with *Tremella aurantia* Schw., descriptions of both species are given below.

Tremella tremelloides (Berk.) Massee. (Fig. 3)

Basidiocarps hemispherical or elongate, expanded and frequently lobate above, contracted into a narrow base below, the lobes free or united marginally, often flattened and crumpled, plicate, rugose, the surface minutely roughened, yellow to bright orange; in section, outer portion gelatinous, the interior with a whitish fleshy layer of varying width; hyphae of both zones compactly arranged, those of the gelatinous portion 2-5μ in diam., with abundant clamps and with haustoria; hymenium consisting of a broad but loosely packed zone of basidia borne at the surface or slightly below it; probasidia

at first clavate or obovate, becoming globose to subglobose or obovate at maturity, longitudinally or obliquely cruciate-septate, 14-22 × 12-18μ, borne terminally and the hyphae proliferating laterally; epibasidia 2.5-6.5μ in diam.; basidiospores globose to broadly ovate, 9-12 × 9-10.5μ.

Type locality:—South Carolina.
Habitat:—Associated with species of *Stereum* on wood of angiosperms.
Distribution:—South Carolina, North Carolina, Tennessee, Iowa, Louisiana and Texas.
Illustrations:—Massee, Jour. Myc. 5, pl. 14, f. 1; Lloyd, Myc. Writ. 3, f. 225; Coker, Jour. Mitch. Soc. 35, pl. 23, f. 1 and pl. 58, f. 2; Bresadola, Icones, pl. 1191; Rogers, Univ. Iowa Stud. Nat. Hist. 15[3], 25, ff. 17-19 and 29, f. 31.

Specimens examined include the type of *Sparassis tremelloides* (K), type of *Naematelia quercina* (NCU) and collections from Iowa, Louisiana, Tennessee and Texas (all IA).

This species does not seem to differ significantly from *Tremella encephala* in its microscopic characteristics. It is possible that the two represent different manifestations of the same species parasitizing two different hosts.

Tremella aurantia Schw. ex Fries, Syst. Myc. 2: 213. 1822. (Fig. 4)

Fructifications typically erect, vesicular-lobate, the lobes crowded, often becoming confluent, hollow, the surface at first minutely roughened, becoming smooth in mature specimens, soft-gelatinous throughout, Orange Buff to Cadmium Orange (Ridgway), fading to pale yellowish on drying; in section, walls of the lobes thick, the hymenium forming an amphigenous layer; hymenium at first covered by a dense layer of conidiophores and conidia, the conidia mostly oval, thin-walled, 3-7 × 2.5-5μ; probasidia at first narrowly clavate, expanding at the apex and becoming capitate or broadly clavate, less commonly ovate or globose, generally with a distinct basal stalk, becoming cruciate or irregularly septate, (13-)15-22(-35) × 10-15(-17)μ, including stalk, forming below the layer of conidiophores and the hymenium thus embedded at first; basidiospores broadly ovate with a large blunt apiculus, (8-)9-10(-11) × 7-8(-9)μ, germinating by repetition.

Type locality:—North Carolina.
Habitat:—Dead wood of angiosperms, associated with species of *Stereum*.
Distribution:—North Carolina, California, British Columbia.

Specimens examined include two collected and identified by Schweinitz, nos. 1107 (Michener Collection, BPI) and 6 (Hooker Collection, K), two specimens from California (IA), and the following from British Columbia; R. J. B. nos. BC-105, -171, -501, -639, -836, -854, -858, -869, and -903.

This species differs from *T. tremelloides* in the size and form of basidia and spores, in lacking a fleshy core and in the possession of a thick layer of conidia in the young basidiocarps. In addition, the

lobes of this species are typically hollow in part, while those of *T. tremelloides* are not.

Naematelia rubiformis Fries, Syst. Myc. 2: 228. 1822.
Tremella rubiformis (Fries) Quél. Fl. Myc. 22. 1888.
Dacrymyces rubiformis (Fr.) Neuhoff, Ark. för Bot. 28A[1]: 51. 1936.

Neuhoff considered *N. rubiformis* Fries to be a *Dacrymyces* and listed *Tremella rubiformis* (Fr.) Quél. (in the sense of Bourdot and Galzin) as a synonym of *T. encephala*. Kennedy (1958) lists *D. rubiformis* (Fr.) Neuhoff as a possible synonym of *D. palmatus* (Schw.) Bres.

Naematelia virescens Corda, Ic. Fung. 3: 35. 1839.
Agyrium atrovirens Fries, Syst. Myc. 2: 232. 1822.
Tremella exigua Desm. Ann. Sci. Nat. III, 8: 191. 1847.
Epidochium atrovirens Fries, Summa Veg. Scand. 471. 1849.
Tremella neglecta Tul. Jour. Linn. Soc. Bot. 13: 34. 1871.
Exidia minutula Sacc. Michelia 1: 502. 1879.
Tremella genistae Lib. ex Roum. & Speg. Rev. Myc. 2: 15. 1880.
Tremella atro-virens (Fries) Sacc. Syll. Fung. 6: 790. 1888.
Tremella atro-virens Fries of various authors, but not of Fries, and not *T. atrovirens* Schum. ex Secr. Mycogr. Suisse 3: 282, 1833.

The name *T. atro-virens* (Fr.) Sacc., generally applied to this species, is a later homonym of *T. atrovirens* Schum. ex Secr. The latter was thought by Secretan to be an alga. Corda's name cannot be transferred, since the combination *T. virescens* has been used for another species (see under *N. virescens* Fries, below). *T. exigua* would then seem to be the earliest acceptable name.

Naematelia virescens (Fries) Fries, Hym. Eur. 696. 1874.
Dacrymyces virescens Fries, Syst. Myc. 2: 229. 1822.
Tremella hemisphaerica Secr. Mycogr. Suisse 3: 288. 1833.
Tremella virescens Bref. Untersuch. 7: 128. 1888.

Brefeld considered his species to be the same as *N. virescens* Corda, but from Corda's illustrations it is apparent that the latter was dealing with *T. exigua* (See under *Naematelia virescens* Corda). Fries (1874) transferred *Dacrymyces virescens* to *Naematelia* and listed Corda's species as being the same. Later authors (Rea, 1922, Bourdot and Galzin, 1928, and Neuhoff, 1936) have treated the two as distinct species, however. Fries is sometimes cited as the authority for *T. virescens*, but, since he apparently never recognized such a combination, this is incorrect.

The proper disposition of the following species is uncertain.

Naematelia coccinea Wettst. Verh. Zool.-Bot. Ges. Wien 35: 554. 1885.

Naematelia granulosa Mont. Ann. Sci. Nat. Bot. IV. 1: 144. 1854.

Naematelia morchellaeformis Kalchbr., listed in Sacc., Syll. Fung. 6: 795. 1888.

Naematelia neglecta Tul. in Lloyd, Myc. Writ. 7: 1150. 1922.

I have not found the original description of this and the name could have been merely a herbarium title.

Naematelia nigrescens Mont. in Gay, Historica fisica y politica de Chile 8:28. 1852.

REFERENCES

BANDONI, R. J. 1958. Some tremellaceous fungi in the C. G. Lloyd Collection, *Lloydia*, **21**:137-151.

BOURDOT, H. AND A. GALZIN. 1928. Hyménomycètes de France iv + 761 pp. Sceaux. Marcel Bry.

BURT, E. A. 1921. Some North American Tremellaceae, Dacrymycetaceae and Auriculariaceae. *Ann. Missouri Bot. Garden*, **8**:361-396.

COKER, W. C. 1920. Notes on the lower Basidiomycetes of North Carolina. *J. Elisha Mitchell Sci. Soc.*, **35**:113-182.

DONK, M. A. 1931. Revisie van de nederlandse Heterobasidiomycetes — en Homobasidiomycetae — Aphyllophoraceae. I. Med. Nederl. *Mycol. Ver.*, **18-20**:67-200.

FRIES, E. 1816. See Liljeblad, S.

———1822. Systema Mycologicum, **2**:1-600.

———1874. Hymenomycetes europaei sive Epicriseos systematis mycologici editio secunda. 1-755.

KENNEDY, LORENE L. 1958. The genus *Dacrymyces*. *Mycologia*, **50**:896-915.

KOBAYASI, Y. 1939. On the genus *Tremella* and its allies from Japan. *Tokyo Bunrika Daigaku Sci. Reports*, **4**:1-25.

LANJOUW, J. AND F. A. STAFLEU. 1956. Regnum vegetabile 6. Index herbariorum 1. The herbaria of the world. 3 ed.

LILJEBLAD, S. 1816. Utkast til en Svensk Flora, ed. 3, Lvii + 763 pp. Upsala.

LLOYD, C. G. 1922. Mycologial Writings, **7**:1149-1150 and 1166.

MARTIN, G. W. 1944. The Tremellales of the north central United States and adjacent Canada. *Univ. Iowa Stud. Nat. Hist.*, **18**(3):1-88.

———1952. Revision of the north central Tremellales. *Ibid.*, **19**:1-22.

NEUHOFF, W. 1936. Die Gallertpilze Schwedens. *Ark. Bot.*, **28**(1):1-57.

OLIVE, LINDSAY S. 1946. New or rare Heterobasidiomycetes from North Carolina — II. *J. Elisha Mitchell Sci. Soc.*, **62**:65-71.

PATOUILLARD, N. 1900. Essai taxonomique sur les familles et les generes des Hyménomycètes. 1-184.

REA, CARLETON. 1922. British Basidiomycetae. Cambridge. University Press. xi + 1-799.

Comments on the Mayfly Genus Campylocia with a Description of a New Species (Euthyplociidae: Euthyplociinae)

LEWIS BERNER[1] and THOMAS B. THEW[2]

ABSTRACT: The status of the mayfly genus *Campylocia* is reviewed and its relationship to *Polyplocia* discussed. Although the two genera are obviously closely related, they can be separated by the use of venational and tarsal differences. *Campylocia* **dochmia,** a new species from Brazil is described.

Several years ago a small collection of mayflies was sent to the senior author by Dr. M. A. V. D'Andretta, Departmento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil. Included in the lot was a series of specimens, mostly males, of *Campylocia* which represents a new species. To clarify our understanding of the new form, it was necessary for us to make a careful study of available specimens of *C. anceps,* a closely related species. Dr. P. J. Darlington, Museum of Comparative Zoology, Harvard College, and Dr. Willis Gertsch, American Museum of Natural History, have kindly loaned us their specimens of *Campylocia.* Further, Mr. D. E. Kimmins, British Museum (Natural History), furnished us with a sketch of the genitalia of *C. anceps* prepared from the holotype and later used in his study of Ephemeroptera types (1960).[3]

Campylocia was first described by Needham and Murphy (1924), and the species, *Euthyplocia guntheri* Navás, 1920, *ampla* n. sp., *anceps* Eaton, 1883, and *burmeisteri* Hagen, 1888, were assigned to it. Subsequently, Gros and Lestage (1926) reviewed the family, erecting a new genus, *Longinella,* for *guntheri* Navás, 1920, and although they showed the species *burmeisteri* in their key to the species of *Campylocia,* they did not list it in their table of genera and species of the Euthyplociidae. Ulmer (1932, 1939, and 1942) considered the genus at some length, pointing out that the position of *burmeisteri* was still not clear but that he (1942, p. 104) would consider it to be a synonym of *anceps* ("Ich halte *Burmeisteri* für identisch mit *anceps*."), a conclusion which we accept. He requested Mr. Nathan Banks' permission to examine Hagen's type in the collection of the Museum of Comparative Zoology, but received no reply. We have been privileged to see this specimen of Hagen's, which has attached to it the following note in Hagen's handwriting: "Not named by Eaton. Forceps figure plate IV. f 7d. It is the third single male he saw." Hagen's specimen belongs to the new species we are describing below.

[1] Department of Biology, University of Florida, Gainesville.

[2] East Moline, Illinois.

[3] Mr. Kimmins wrote to us with reference to the wings of *C. anceps,* "I have compared the wings of the type with Eaton's figure and consider that he has drawn them accurately."

In 1932 Ulmer concluded that *Longinella* Gros and Lestage = *Campylocia,* thus properly establishing the generic placement of *guntheri* Navás. Further, Ulmer (1942) synonymized *intercalata* Banks, 1918, *guntheri,* and *ampla* Needham and Murphy with *anceps.* No other species have been described in the genus since that date. *C. sikorai* (Vayssière) from Madagascar is retained in the genus by Demoulin (1952).

The most recent review of *Campylocia* is given by Demoulin (1952 and 1953) in which he presents a key to the subfamily *Euthyplociinae.* He differentiates *Campylocia* from *Polyplocia* Lestage, 1921, by claiming that in the mesothoracic wings the bifurcation of MA is clearly beyond that of Rs in *Campylocia* while in *Polyplocia* the bifurcation is practically at the same level. Further, he characterizes both genera as having four-segmented tarsi on the meso-and metathoracic legs. In his discussion of *Campylocia,* he shows that the venation in the wings of *C. anceps* is highly variable in the development of the marginal intercalaries of the radial, anterior median, and posterior median spaces. He cites Ulmer (1939) as doubting the position of the forking of MA and Rs being of any significance in separating the two genera and states that he is in agreement with this conclusion. However, he does believe that the position of the two cubital intercalaries are of much greater value in separating the two genera. In *Polyplocia* the cubitals join CuP, but in *Campylocia* only the longer joins CuA and is generally separated from CuP by at least a sigmoidal vein.

A careful study of our new species clearly indicates that Ulmer is correct in his doubts about the position of the forking of Rs and MA, as in the forewings of our form it occurs at the same level. This character is therefore no longer of use in differentiating *Campylocia* from *Polyplocia,* and if the two genera are really distinct, the only venational characteristic which will serve to separate them is that pointed out by Demoulin and described above.

Ulmer's (1942) detailed analysis of the venation of *C. anceps* clearly shows the degree of variability that is found in the forewing of this species. Our studies of Spieth's specimens reveal that the venational variations are consistent with Ulmer's drawings, especially with reference to the presence of one or two cubital intercalaries. Specimens, apparently taken at the same place and same time, show either one or two of these veins. Where there is a single intercalary it is attached to CuA, while if the second is present it is attached to the first and longer of the two. We have also noted that the forking of Rs and MA is variable as to the distance MA forks distally to Rs. In some of the American Museum specimens, the level of forking is separated by less than the distance of one crossvein from another while at the opposite extreme the forking may be as many as three crossveins apart.

In every available specimen of the species described below as *C. dochmia,* the forks of Rs and MA are virtually at the same level.

Whether this character alone would be of sufficient value to separate this species from *anceps* is questionable.

The metathoracic wing of *Campylocia* has IMP attached to MP_1, CuA, or unattached. Generally MP_2 is attached to CuA and does not fork with MP_1. Again, because of the variability of these veins it may not be correct to use their points of attachment as a generic characteristic. Ulmer's (1939) and Demoulin's (1952) drawings of hindwings of *Polyplocia* show that IMP is attached to MP_2 and MP has normal forking.

While studying the legs of *C. dochmia,* we discovered that the tarsi of the mesothoracic legs are five-segmented rather than four, as claimed by Demoulin for *Campylocia* and *Polyplocia* in his key to the genera. To establish the constancy of this characteristic, we have examined legs from several specimens of *C. anceps* (one of the specimens described as *C. intercalata* by Banks, and several specimens from British Guiana and Surinam which had been studied by Spieth, 1943) and in every case the midtarsus was consistently five-segmented. Whether the discrepancy in the number of tarsal segments on the mesothoracic legs can be used as a further means of distinguishing these two closely related genera must await a study of specimens of *Polyplocia.*[4]

The genitalia of *C. anceps* have been figured by several authors with some apparent differences. The illustration published by Kimmins (1960) should establish with certainty the species with which Eaton was working. Spieth's drawings, made from specimens collected in Venezuela and Surinam, show more details of the genitalic structures. The dome-shaped subanal plate in Spieth's drawing is also variable and the posterior edge of this structure may range from being almost truncate to as curved as illustrated by him. In *C. dochmia* the posterior edge of the subanal plate is broadly truncate and slightly emarginate. The penes of the two species are distinctive, those of *dochmia* having medial lobes that are lacking in *anceps.* A comparison of the genitalia of *dochmia* with Eaton's (1883) figure 7d, Plate IV, leads us to believe that he was dealing with the same forms we are describing below. Although details are lacking in this illustration, the shape of the subanal plate, as he shows it, is very similar to that of *dochmia.*

Table 1 shows that both males and females of *C. dochmia* are generally larger than *C. anceps.* Measurements of *dochmia* were difficult to make because of the way in which the specimens were preserved. The wings were crumpled when the insects were placed in alcohol by packing the whole series in a single vial. Attempts to straighten them for measuring almost always resulted in tearing the

[4] Dr. Demoulin (personal correspondence, February 15, 1961) has kindly re-examined his specimens of *Polyplocia* and confirmed that the second leg has four movable segments. Segment one is not defined on the dorsal surface of the tarsus and is fused to the tibia on the ventral side. Obviously it is not movable.

membrane. The posterior part of the abdomen of the females is recurved over the back so that their body length cannot be measured with any degree of accuracy.

TABLE I.—A comparison of the size of *Campylocia anceps* and *C. dochmia* (all measurements in millimeters)

	Wing		Body		Caudal filaments	
	Male	Female	Male	Female	Male	Female
*C. anceps**	10-14.5	15-32	11-12	22-26	35	
*C. anceps***	13-22	34	12-20		55	
C. dochmia	19-22.5	31-35	15-22	22?	52-62	56-64

* Measurements given by Spieth (1943).
** Measurements given by Ulmer (1942). He lists the wing length of only the largest female.

Campylocia dochmia, sp. nov.

MALE

Measurements.—Body-15.0-22.0 mm; forewing-19.0-22.5 mm; hindwing-8.5-9.5 mm; caudal filaments-52-62 mm.

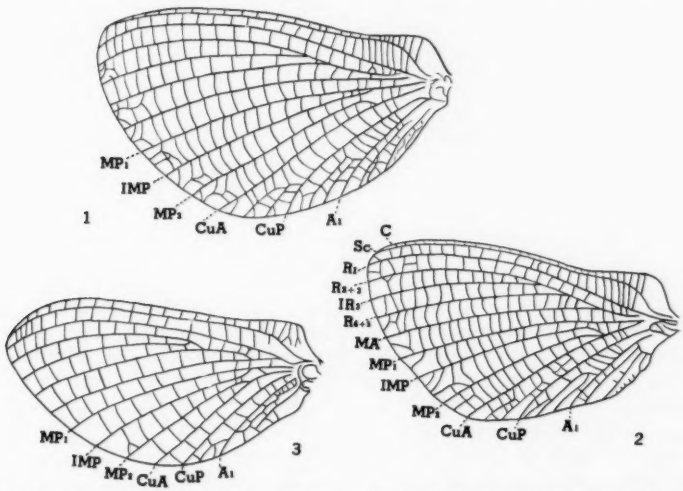
Head.—Purplish brown; vertex between compound eyes heavily shaded with black and with margins and paramedian longitudinal ridges deep purple; occiput light brown with extreme lateral areas and posterior margin suffused with dark purple and with two dark paramedian longitudinal stripes; face and vestigial mouth parts yellowish white, marked with purple. Antennal scape yellow, shaded with purple; pedicel light brown, with several purple longitudinal stripes; flagellum light brown, except whitish near base. Ocelli pale, ringed with deep purple at base. Compound eyes black and placed on stalk-like projections from vertex.

Thorax.—Light brown, with general suffusion of dark purple. Pronotal maculation composed of two areas; anterior one-fourth light brown, suffused with purple, with two small rounded indentations into lateral areas of second, darker area; anterior margin dark; posterior three-fourths of pronotum light purplish brown, with lateral and anterolateral margins dark and with dark transverse stripe on each side paralleling the posterior margin, but some distance from it; from each lateral indentation of first area to this transverse stripe, an oblique lighter area, bounded with purple-brown, which combines with transverse stripe where they meet to form black-brown oblong mark; median area pale, bound with dark brown, which is especially heavy anteriorly, where it is stippled with light brown; immediately lateral to this pale area anteriorly and adjacent to oblique light area, a small light brown triangle, finely bordered with purple; pleura light brown, marked with brown; prosternum yellow-white, suffused with very light purple and with sutures marked with dark purple. Mesonotum light brown, with general purplish suffusion and with

sutures purple; prescutellar and posterior paramedian sutures dark purple; scutellum light brown; triangular area of light brown present on posterolateral areas of scutum; pleura light brown, marked with dark purple, especially around wingbase and coxae; upper anterior region purple, stippled with light brown; mesosternum light brown, suffused with darker brown and with sutures purple; basisternum white, with mediolateral and posterolateral light brown blotches; immediately lateral to the posterior pair, a pair of purple blotches (outside of basisternum). Metanotum light yellow-brown, with median area hyaline and with posterior margin and posterolateral sutures dark purple; pleura and sternum as in mesothorax, except upper anterior region of pleura light brown.

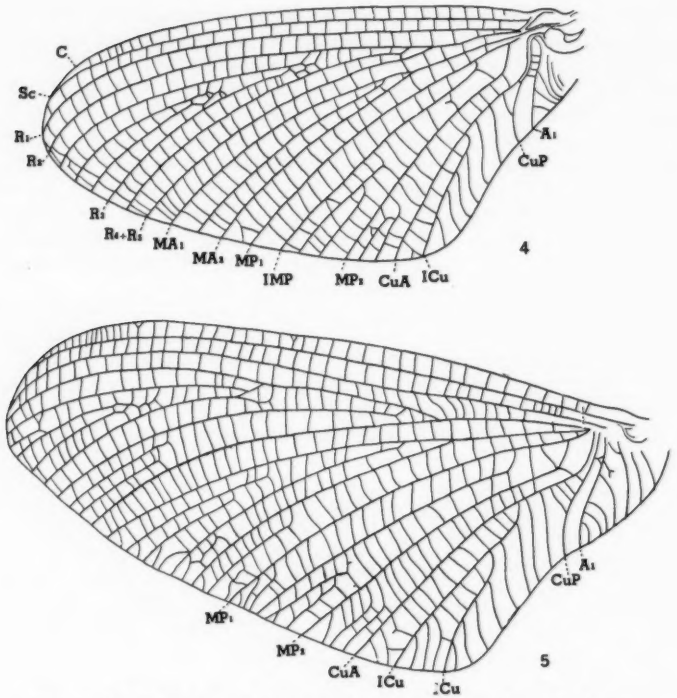
Wings.—Translucent, with purplish tinge, which is especially heavy in costal and subcostal interspaces in forewing. Longitudinal veins light purple; crossveins purplish. Venation as in Figs. 1, 2 and 5.

Legs.—Measurements: foreleg-16.3 mm; femur-4.5 mm; tibia-5.8 mm; tarsus-I-0.4 mm, II-2.1 mm, III-1.3 mm, IV-1.2 mm, V-1.0 mm; midleg-7.7 mm; femur-3.5 mm; tibia-3.1 mm; tarsus-1.1 mm; hind-



Figs. 1-3.—Hindwings of *Campylocia*. 1. *C. dochmia* with IMP attached to MP_1 and MP_2 attached to Cu A. 2. *C. dochmia* with both IMP and MP_2 attached to Cu A. 3. *C. anceps* from Surinam.

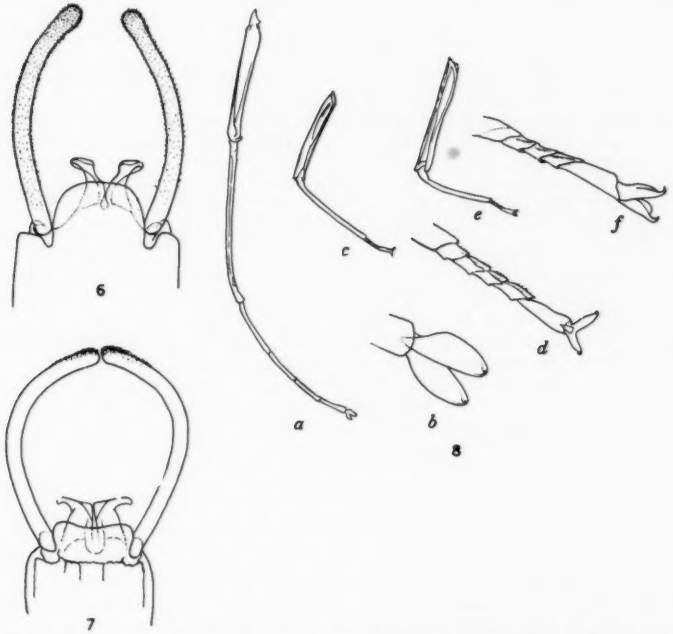
leg-8.2 mm; femur-4.3 mm; tibia-3.0 mm; tarsus-0.9 mm. Coloration: foreleg dark purplish brown; femur and tibia with dark longitudinal streaks; tarsal joints whitish and tarsal claws yellow. Mid-and hindlegs similar, except femur shaded with lighter purple. Legs and tarsal claws, as in Figs. 8a, c, e and 8b, d, f.



Figs. 4-5.—Forewing of *Campylocia*. 4. *C. anceps* from Surinam. 5. *C. dochmia*.

Abdomen.—Tergites purplish brown, stippled with pale brown and with median stripe, which is hyaline on anterior segments; anterior margin whitish, posterior pale brown; paramedian light, oblique stripe pointing to posterolateral corners, the extreme anterior and posterior ends of which are paler and thus appear as spots; oblique pale stripe arising from anterolateral corners and pointing inward, from the ends of which several very narrow, vine-like lines proceed medially; also, a small pale spot adjacent and slightly lateral to terminal end of this stripe; tergite 9 darker and with markings reduced; tergite 10 slightly paler than 9, with median and lateral stripes of pale brown and with dark brown oblique stripe arising from blackish area adjacent to anterior end of lateral stripes and ending at posterior end of median stripe; posterior margin brownish hyaline. Posterior margin of tenth tergite deeply incised producing broadly rounded median lobe and smaller lateral lobes separated by pale brown grooves. Pleura brownish, with dark brown spiracular markings. Venter pale brown hyaline, generally suffused with brown

laterally, which gradually becomes heavier and more inclusive posteriorly; posterior margin finely bordered with light brown.
Genitalia.—Yellowish white, tinged with purple, as in Fig. 7; forceps shaded with purple.
Caudal filaments.—Purplish, darker basally; joints pale.



Figs. 6-8.—Genitalia and legs of *Campylocia anceps* and *C. dochmia.* 6. Genitalia of *C. anceps* from Venezuela. 7. Genitalia of *C. dochmia.* 8. Legs of *C. dochmia.* a. foreleg, b, tarsal claws of foreleg, c. middle leg, d. tarsus of middle leg, e. hindleg, f. tarsus of hindleg.

FEMALE

Similar to male, with the following exceptions:
Measurements.—Body-22.0 mm?; forewing-31.0-35.0 mm; hindwing-13.8 mm; caudal filaments-56-64 mm. Pronotum with first light colored area extremely reduced; posterior area darker than in male, but with substantially the same pattern. Abdomen with same general maculation as male, but darker.

Holotype, male.—Brazil, Est. Minas Geraes, Sapucai-mirim (Cidade Azul-1400 mts.), Trav. F°. Nov. 5, 1953. C. Gans and S. Medeiros, collectors. Taken at light and preserved in alcohol. No. 3362.0, University of Florida Collections.

Allotype, female.—Same data as for holotype. No. 3362.0, University of Florida Collections.

Paratypes.—21 males, 1 female. Same data as for holotype. 14 males, 1 female in the University of Florida Collections; 2 males in the collection of Thomas B. Thew; 3 males in collection of Dr. George Edmunds, University of Utah; 2 males in collection of Departamento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil.

REFERENCES

BANKS, NATHAN 1918. New neuropteroid insects. *Bull. Mus. Comp. Zool.*, **62**(1):1-22, pls. 1-11.

DEMOULIN, GEORGES 1952. Contribution a l'étude des Ephoronidae Euthyplociinae (insectes Éphéméroptéres). *Bull. Inst. Roy. Sci. Nat. Belg.*, **28**(45):1-22, 5 figs.

———1953. A propos des *Polyplocia* de Borneo (insectes Éphéméroptéres). *Ibid.*, **29**(19):1-4, 1 fig.

EATON, A. E. 1883. A revisional monograph of recent Ephemeridae or mayflies, Part 1. *Trans. Linnean Soc. Lond.*, 2nd Ser., **111**:1-77, pls. I-IV.

GROS, A. J. AND J. A. LESTAGE 1926. Contribution a l'étude des larves des Éphéméroptéres. Serie IV. Le groupe Euthyplocien. *Ann. Biol. Lacustre*, **15**:119-162, 20 figs.

KIMMINS, D. E. 1960. The Ephemeroptera types of species described by A. E. Eaton, R. McLachlan, and F. Walker. *Bull. Bri. Mus.* (Nat. Hist.), **9**(4):269-318, 65 figs.

LESTAGE, J. A. 1921. Les Ephéméres Indo-Chinoises. *Ann. Soc. Ent. Belg.*, **61**(V-VI):211-222.

NAVÁS, R. P. L. 1920. Algunos insectos del Brasil. *Rev. Mus. Paulista*, **XII**:287-291, 2 figs.

NEEDHAM, J. G. AND H. E. MURPHY 1924. Neotropical mayflies. *Bull. Lloyd Libr., Ent. Ser. 4., Bull.* **24**:1-79, pls. I-XIII.

SPIETH, H. T. 1943. Taxonomic studies on the Ephemeroptera. III. Some interesting ephemerids from Surinam and other Neotropical localities. *Amer. Mus. Novitates*, **1244**:1-13, 21 figs.

ULMER, GEORG 1932. Bemerkungen über die seit 1920 neu aufgestellten Gattungen der Ephemeropteren. *Stett. Ent. Zeit.*, **93**:204-219.

———1939. Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. *Arch. Hydrobiol.* Suppl., **16**:443-692, 469 figs.

———1942. Alte und neue Eintagsfliegen (Ephemeropteren) aus Süd-und Mittelamerika. *Stett. Ent. Zeit.*, **103**:98-128, 32 figs.

Cyprinid Fishes of the Subgenus Cyprinella of Notropis. IV The Notropis galacturus—camurus Complex

ROBERT H. GIBBS, JR.
Department of Biology, Boston University, Boston 15, Massachusetts

ABSTRACT: The species *Notropis galacturus* and *N. camurus* are redescribed and differentiated from other species of the subgenus *Cyprinella* and synonymies are given. These two species form a distinct unit within the subgenus, distinguished by the presence of depigmented basicaudal areas, a hiatus between nuptial tubercles of the snout and those of the top of the head, two rows of tubercles on each chin ramus, and red pigment in dorsal and anal fins of breeding males. Populations of *N. galacturus* east and west of the Mississippi have differentiated slightly. Lower Mississippi populations of *N. camurus* are racially distinct from those in the Arkansas system. The two species are probably derived from a common stock which became divided into eastern and western portions. *N. galacturus* has crossed the Mississippi, but the range of *N. camurus* appears to have contracted, leaving the two present populations.

The systematic situation in the subgenus *Cyprinella* has been outlined in the first paper of this series, and the two variable species *N. spilopterus* and *N. venustus* treated in subsequent parts (Gibbs, 1957a, b, c). *Notropis galacturus* and *Notropis camurus* stand apart from most of the species of *Cyprinella* as a unit, defined by a number of characters which they have in common. First, and most notable, both have depigmented areas at the caudal base which, at their fullest development, are quite prominent. Occasionally in other species of *Cyprinella* a specimen is found which has such depigmentation, but the character is never common. An unrelated species which is sympatric with *N. galacturus* in the Tennessee system, *Notropis coccogenis,* also has prominent depigmented caudal areas, but this is surely a case of parallelism. The breeding males of both *N. galacturus* and *N. camurus* have greatly enlarged dorsal fins and red pigment in both dorsal and anal. Their tubercle patterns are similar, notably in the lack of a hiatus between the tubercles of the top of the head and those of the snout, in the minuteness of the nape tubercles, and in the presence of two rows on each chin ramus.

This paper redescribes the species *N. galacturus* and *N. camurus,* treats their intraspecific variation, and discusses their possible origin and means of dispersal.

MATERIALS AND METHODS

Specimens used in this study were from the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Cornell University; University of Georgia; Museum of Zoology, University of Michigan; Tulane University; and United States National Museum

(USNM). To staff members of these institutions, I owe my deepest appreciation.

Counts and measurements were made in accordance with Hubbs and Lagler (1958), except postdorsal length (dorsal origin to caudal base) and dorsal origin to lateral line. All measurements were made on specimens between 50 and 60 mm, and are recorded as per cent of standard length.

This paper is based on a doctoral thesis, done at Cornell University under Dr. Edward C. Raney. To him, and to the many colleagues who gave constructive criticism or aid in the field, I extend my sincere thanks.

Notropis galacturus
Whitetail Shiner

Hypsilepis galacturus. Cope, 1867:160 (orig. descr.; Holston system, Va.); 1869:229 (Holston system, Va.), 1870:459 (French Broad, Clinch, Cumberland systems).

Leuciscus kentuckiensis. Günther, 1868:251 (specimens from Cope from Holston R.).

Cyprinella galactura. Jordan and Copeland, 1876:153; Jordan, 1929:81 (char., distr.); Pratt, 1935; 76 (char., distr.); Schrenkeisen, 1938:130 (char., distr.).

Luxilus galacturus. Jordan, 1877:339, 370, 373 (Tennessee and Cumberland systems); 1878a:294 (char., distr.); 1878b:421, 1879:110 (distr.).

Photogenis galacturus. Jordan and Brayton, 1878:18, 64, 91 (Tennessee, Cumberland and Savannah systems).

Hudsonius galacturus. Jordan, 1880:292 (char., distr.); 1884:292 (char., distr.).

Cliola galactura. Jordan and Gilbert, 1883:179 (char., distr., syn.).

Notropis galacturus. Jordan, 1885:814; Call, 1887:76 (Shannon Co., Mo.); Jordan and Gilbert, 1887:2 (White R., Ark.); Jordan, 1889:145, 152 (Holston and French Broad systems); Gilbert, 1891:147 (Tennessee system, Ala.); Meek, 1891 (Neosho, White and Black systems, Ark. and Mo.); Kirsch, 1892:291 (Cumberland system, Ky.); Woolman, 1892:266 (Cumberland system, Ky.); 1893:260-267 (Cumberland system, Ky. and Tenn.); Evermann and Kendall, 1895: 470 (White system, Mo.); Meek, 1895:77, 82 (White system, Ark.); Jordan and Evermann, 1896b:256 (distr., syn.); 1896a: 257 (char., distr., syn.); Smith, 1907:93 (French Broad system, N.C.); Goldsborough and Clark, 1908:35 (Monongahela system, W. Va. — doubtful); Fowler, 1910:283 (variation); Jordan, 1910:58 (char., distr.); Cockerell, 1911:384 (scale illustrated); Evermann and Hildebrand, 1916:444 (E. Tenn.); Jordan, 1916 (char., distr.); Evermann, 1918:364 (Ky. and Tenn.); Fowler, 1923:16 (Catawba doubtful and French Broad systems, N.C., Cumberland system, Tenn.); Pratt, 1923:80 (char., distr.); Pickens, 1928:30 (S.C.); Hildebrand, 1932:66 (Tuckasegee R., N.C.; char.); Kuhne, 1939:50 (Tenn.); Shoup and Peyton, 1940:111, 113 (Cumberland system, Tenn.); Shoup, Peyton and Gentry, 1941:69 (Obey R., Tenn.); Fowler, 1945:115, 343 (N.C., Ala.).

Erogala galactura. Jordan, Evermann and Clark, 1930:129 (distr., syn.); Fowler, 1936a:192 (Holston system, N.C.); 1936b:111 (Charter, Tenn.); Driver, 1942:274 (distr., char.); 1950:287 (char., distr.).

Types.—One specimen of *Hypsilepis galacturus,* collected by Prof. E. D. Cope in North Carolina, is located in the U.S. National Museum. This specimen, a male, 83.8 mm, USNM 14981, is herein designated lectotype. In the Academy of Natural Sciences at Philadelphia there are 64 syntypes, ANSP 3381-3444, collected by Cope in the Holston River, Virginia.

Collections examined by river system.—Savannah, 1; Santee, 1; Tennessee, 92; Cumberland, 14; White, 52; St. Francis, 4; Mississippi, 1. Kanawha system collections not seen.

Comparative diagnosis.—*Notropis galacturus* occurs sympatrically with *N. s. spilopterus, N. whipplei,* and *N. v. venustus* of the subgenus *Cyprinella.* There are few records of its being taken with *N. camurus,* although in the White system there is apparently a small, perhaps introduced, population of *N. camurus* together with the abundant *N. galacturus.* The differentiation of *N. galacturus* from *N. camurus* may be seen in Tables I-IV. *N. camurus* has fewer lateral-line scales, a smaller predorsal length, accompanied by a longer postdorsal length, a longer head, generally deeper body, as expressed in body depth, dorsal origin-lateral line and caudal peduncle depth, and a slightly larger orbit and longer upper jaw. In addition, the depigmented caudal base of *N. camurus* is much less bipartite than that of *N. galacturus,* often appearing as a bar across the base of the fin rays, and the snout is extremely blunt.

N. whipplei, and particularly *N. spilopterus,* are likely to be the most confusing species. Specimens of *N. galacturus* which have less-prominent depigmented caudal areas very strongly resemble *N. spilopterus,* and in fact, this study has revealed specimens which are surely hybrids between the two.

In the river systems east of the Mississippi, *N. galacturus* differs from *N. s. spilopterus* in the following characters: (1) usually 39-41 laternal-line scales instead of 37-39, (2) usually 15 or 16 pectoral rays, instead of 13-15, (3) a more slender body, usually 21-23% of standard length, instead of 22-26% (4) caudal peduncle depth usually 10-11% of standard length, instead of 11-12%, (5) pigment present along base of anal fin and along the midventral caudal peduncle, (6) the presence from an early age of at least a moderate amount of pigment in all dorsal fin membranes, while *N. spilopterus,* except in breeding males, has little or no pigment in the first three membranes, and (7) the presence of depigmented basicaudal patches.

In the same eastern systems and also west of the Mississippi, *N. galacturus* differs even more trenchantly from *N. whipplei* in most of the same characters. *N. whipplei* has: (1) usually 37 or 38 lateral-line scales, (2) usually 14-16 pectoral rays, (3) body depth 24-28% of standard length, (4) caudal peduncle depth 10-12% of standard length, (5) no pigment along anal base or midventral caudal peduncle, (6) pigment in all dorsal membranes, thus not differing from *N. galacturus,* and (7) no depigmented basicaudal patches.

West of the Mississippi, *N. galacturus* may be distinguished from *N. spilopterus hypsisomatus,* with which it is not sympatric, by its greater number of lateral-line scales, 39 or 40, instead of 35-38; by its 15 or 16 pectoral rays, instead of 13-15; by its smaller body depth, 19-22% of standard length, instead of 10-13%; and by its smaller distance from dorsal origin-lateral line, 12-15% of standard length, instead of 14-19%. In pigmentary differences, the two forms may be told apart as in the comparison of *N. s. spilopterus* and *N. galacturus* above.

Notropis v. venustus, the only remaining *Cyprinella* likely to be confused, has a prominent black caudal spot which *N. galacturus* lacks, and itself lacks the depigmented basicaudal patches of *N. galacturus.*

It might be possible to confuse *N. galacturus* in the Tennessee and Cumberland with *Notropis coccogenis,* which is not a species of *Cyprinella,* but which has a depigmented caudal base. *N. coccogenis* has 2,4-4,2 teeth, and lacks the distinctive *Cyprinella* characters of narrowly outlined scales which appear diamond-shaped, and contrastingly dark posterior dorsal membranes. It further lacks tubercles on top of the head, these being present only at the tip of the snout and lower jaw.

Description.—Teeth 1,4-4,1, hooked, the grinding surfaces narrow, elongate, concave, and usually not serrated. Anal rays 9. Pectoral rays usually 15 or 16. Lateral scales with exposed portions higher than wide. Lateral-line scales usually 39-41; predorsal circumferential scales 13-2-11; caudal peduncle scales 7-2-5. No crowding before dorsal. Dorsal fin moderate in size in non-breeding adults, the first or second principal ray longest, the middle rays longest in the depressed fin; origin nearer caudal base than snout tip.

Head subconical. Orbit usually about 7% of standard length, shorter than snout, 3-4 in head. Mouth terminal or subterminal, oblique, moderate in size; upper jaw reaches about to level of anterior edge of orbit. Upper jaw slightly longer than either lower jaw or orbit. Body, slender, terete, body depth usually 20-23% of standard length. Caudal-peduncle depth usually 10-11% of standard length. Lateral line slightly decurved from opercular margin to below middle of dorsal fin.

Breeding males with scattered tubercles on top of head, snout, and area between eye and snout, most dense in the latter two areas. No hiatus present between head and snout tubercles. Chin rami with two or more rows smaller than those of top of head. Nape tubercles very small; those of rest of notal ridge absent or almost invisible. Extremely small prickles on all body scales except belly, partially arranged in rows on exposed scale margins. Small tubercles on all fin rays, following their branching, often weak in dorsal and caudal.

Coloration.—Dorsal scales and a row or two below the lateral line narrowly edged in black, appearing diamond-shaped. A poorly developed lateral stripe present behind the level of the dorsal fin, the

narrow dark line which marks its dorsal outline continued forward almost to opercle. A very diffuse band, slightly denser than the background color, runs in a straight line from opercle to caudal base, its lower half merging with the lateral stripe posteriorly. A narrow middorsal line present along entire dorsum both before and behind dorsal fin.

The most prominent character of the species is the depigmented caudal base, which takes the form of two patches whose margins extend from the bases of the most-anterior procurrent rays to the middle of the junction between scales of caudal peduncle and caudal rays, and out to the distal end of the longest procurrent ray (see Fig. 1).

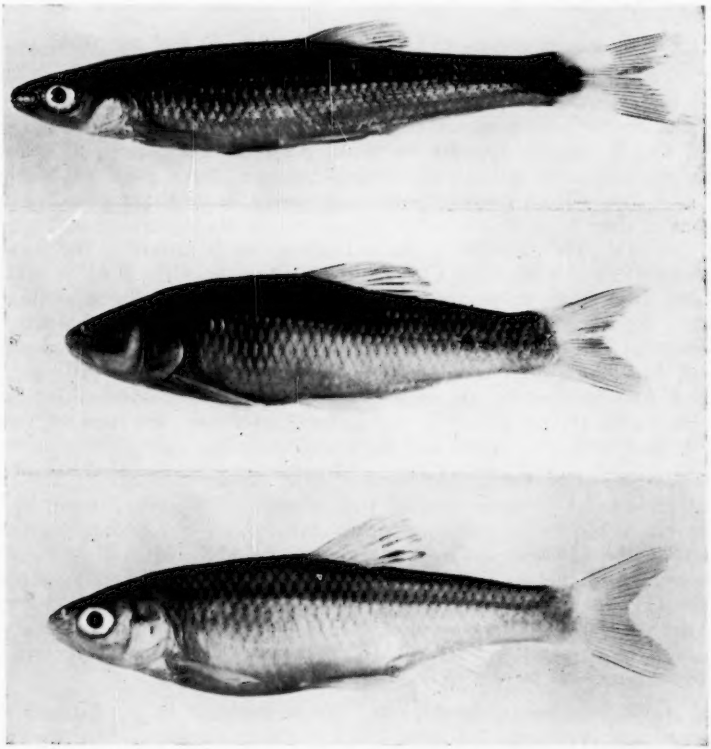


Fig. 1.—Left lateral views of: (top) *Notropis galacturus*, CU 25992, male, 60.3 mm, Tennessee drainage, Franklin Co., Tenn.; (middle) *N. camurus*, CU 23357, male, 61.1 mm, Arkansas drainage, Cherokee Co., Okla.; (bottom) *N. camurus*, CU 24931, female, 64.7 mm, Mississippi drainage, De Soto Co., Miss. Photography by Douglass M. Payne of Cornell University.

Belly immaculate. Sides of anal fin and midventral caudal peduncle with more or less prominent pigment.

Top of head dark, covered with small melanophores which reach the lower edge of the lachrymal and circle the eye. The upper part of the preopercle and the entire opercle are covered with diffuse, larger melanophores. The pigment of the lips is similar to that of the snout. Remainder of head immaculate. Deep-lying bar of pigment between chin rami hardly visible.

Dorsal fin usually well pigmented on all membranes, the last two noticeably darker than the rest. Caudal lightly pigmented except in basal patches, the pigment along outer edges of rays often very dark, adding to the contrast of the depigmented areas. Pectoral fin rays usually with melanophores lining the leading rays. Pelvics and anal lack pigment.

Breeding males assume a dusky gray cast, all fins are filled with milky pigment, and the anal and enlarged dorsal fin are red.

Infraspecific variation.—Exchange of genetic material between stocks of *N. galacturus* in the Tennessee-Cumberland and those in the Ozark region appears to have been sufficient and/or recent enough to minimize the differences between these portions of the range. Fishes from the two regions, however, show slight but definite signs of drift from one another. These trends are illustrated in Tables I, III, IV. The number of lateral-line scales is different, the mean being 39.50 or less in the Ozarks, 40.00 or more in the East. A slight trend is present in pectoral rays, of which the Ozark populations have slightly more than the East. Among proportional characters, predorsal length, head length, caudal peduncle depth, body depth, and dorsal origin-lateral line show a shift. None of these differences is of such magnitude as to warrant nomenclatorial recognition, or even racial status, although the latter, merely on the basis of geographical isolation would not seem unreasonable.

Range.—Tennessee, Cumberland, and upper Savannah, Santee, and Kanawha systems east of the Mississippi; Ozark Plateau and Ouachita Mountain portions of the White and St. Francis systems west of the Mississippi. One collection in the U.S. National Museum, according to the accompanying data, was made in Wyatt, Missouri. Wyatt is in Mississippi County and is well outside the range of either eastern or western segment of the species. Further, *N. galacturus* habitat is probably not found in this region. Although the record is possible, it must be the subject of considerable doubt.

Habitat.—Cool, clear streams, most commonly in the vicinity of mountains. Although it is most often found in moderate-sized waters, it has been taken on occasion in small headwater streams.

Etymology.—The name *galacturus* is derived from the Greek *gala* (genetive *galactos*), milk and *oura*, tail, with reference to the white basicaudal marks.

TABLE I.—Frequency distribution of meristic characters *of Notropis galacturus* and *N. camurus*

River System	Lateral-line scales												
	35	36	37	38	39	40	41	42	43	N	$\bar{x}$	SD	SE
N. galacturus													
Cumberland	....	....	....	....	13	33	13	1	....	60	40.0	.71	.09
Tennessee	....	....	....	2	36	116	76	16	4	250	40.3	.88	.06
Savannah	....	....	....	....	....	....	1	....	....	1	41.0	....	....
White	....	....	....	5	34	32	3	1	....	75	39.5	.75	.09
St. Francis	....	....	....	....	4	1	1	....	....	6	39.5	.84	.34
(Mississippi)	....	....	....	1	4	3	....	....	....	8	39.3	.71	.25
Total eastern	....	....	....	2	49	149	89	18	4	311	40.3	.86	.05
Total western	....	....	....	5	38	33	4	1	....	81	39.5	.75	.08
N. camurus													
Osage	....	4	1	....	....	....	....	....	....	5	36.2	.45	.20
Arkansas	3	91	60	5	....	....	....	....	....	169	36.3	.76	.04
Total Arkansas Race	13	95	61	5	....	....	....	....	....	174	36.3	.66	.05
Lower Miss. Race	....	10	45	29	2	....	....	....	....	86	37.3	.69	.05

N. galacturus	Pectoral rays									
	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Cumberland	....	12	58	43	6	....	119	15.4	.73	.07
Tennessee	....	59	271	167	16	1	514	15.3	.71	.03
Savannah	....	....	....	2	....	....	2	16.0	....	....
White	....	9	72	79	10	....	170	15.5	.69	.05
St. Francis	....	....	6	5	1	....	12	15.6	.67	.19
(Mississippi)	....	....	9	6	....	....	15	15.4	.51	.13
Total eastern	....	71	329	212	22	1	635	15.3	.72	.03
Total western	....	9	78	84	11	....	182	15.5	.69	0.5
N. camurus										
Osage	....	....	6	4	....	....	10	15.4	.52	.16
Arkansas	4	19	145	150	26	....	344	15.5	.76	0.4
Total Arkansas race	4	19	151	154	26	....	354	15.5	.76	.04
Lower Miss. race	....	11	81	77	9	....	178	15.5	.69	.05

Notropis camurus (Jordan and Meek)
Bluntface Shiner

Cliola camura. Jordan and Meek, 1885:474 (orig. descr.; Fort Lyon, Colo.).
Notropis camurus. Cragin, 1885:108 (Neosho system, Kans.); Jordan, 1885:814; 1891:18 (Arkansas R., Wichita, Kans.); Gilbert, 1886:208 (Neosho R., Oswego, Kans.); Jordan and Evermann, 1896b:256 (distr., syn.); 1896a:279 (char., distr., syn.); Gilbert, 1889:39 (Neosho system, Kans.); Jordan, 1899:58 (char., distr.); 1910:58 (char., distr.); 1916:58 (char., distr.); Pratt, 1923:80 (char., distr.); Jordan, 1928:370 (distr.); Moore and Paden, 1950:85 (Illinois R., Okla.); Moore, 1952 (Okla.).
Cyprinella whipplei. Graham, 1885:73 (misidentification).
Erogala camura, Jordan, Evermann and Clark, 1930:129 (distr., syn.).

TABLE II.—Frequency distribution of meristic characters of *Notropis galacturus* and *N. camurus*

River System	Pred. circumf. scales above LL					N
	11	12	13	14	15	
N. galacturus						
Cumberland	....	....	55	2	3	60
Tennessee	8	9	215	11	12	255
Savannah	....	....	1	....	....	1
White	....	....	58	6	12	76
St. Francis	....	....	6	....	....	6
(Mississippi)	....	....	5	1	2	8
Total eastern	8	9	271	13	15	311
Total western	....	....	64	6	12	82
N. camurus						
Osage	....	....	1	1	3	5
Arkansas	....	1	85	41	43	170
Total Arkansas Race	....	1	86	42	46	175
Lower Miss. Race	3	4	76	3	1	87

River System	Anal rays		N
	8	9	10	
N. galacturus				
Cumberland	....	56	3	59
Tennessee	18	228	11	257
Savannah	....	1	....	1
White	6	78	2	86
St. Francis	....	6	....	6
(Mississippi)	....	8	....	8
Total eastern	18	295	14	317
Total western	6	84	2	92
N. camurus				
Osage	....	5	....	5
Arkansas	9	157	5	171
Total Arkansas Race	9	162	5	176
Lower Miss. Race	....	81	8	89

Cyprinella camura. Pratt, 1935:76 (char., distr.); Schrenkeisen, 1938:130 (char., distr.).

Notropis camura. Cross, 1954:309 (Neosho system, Kans.).

Types.—*Cliola camura* Jordan and Meek USNM 15256. Fort Lyon, Colo., Lr. E. Palmer. Two specimens were in this type series. One of these, a very highly developed male, 80.0 mm in standard length, with an extremely arched dorsal profile, is herein designated lectotype and retains the original catalogue number. The other is a specimen which had previously been reidentified as *Hybognathus nuchalis placita.* This has been recatalogued as USNM 163962.

Collections examined by river system.—Arkansas, 61; White, 1; Osage, 1; Lower Mississippi tribs. in Miss. and La., 25.

Diagnosis.—Although *Notropis camurus* is sympatric with only two species of *Cyprinella, Notropis spilopterus hypsisomatus* and *Notropis v. venustus,* it actually most closely resembles *N. whipplei.*

One would be hard-put to distinguish *N. camurus* from *N. whipplei* on the basis of meristic characters, and proportional characters show few distinctions. The head length is usually 26-28% of standard length in *N. camurus,* instead of 25-26%, and the upper jaw is usually 8-9% of standard length, instead of 8%. Thus it is clear that identification must rest on conformation and coloration. *N. camurus* has the depigmented caudal base, which *N. whipplei* lacks, and has a much blunter snout, although the Lower Mississippi form of *N. camurus* is less extreme in the latter character. Breeding males of *N. camurus* may be distinguished by their red dorsal and caudal fins, and by the lack of a hiatus between tubercles of head and snout (Fig. 2).

From *Notropis spilopterus hypsisomatus, N. camurus* may be identified by its 15 or 16 pectoral rays, instead of 13-15; by its larger upper jaw, usually 8-9% of standard length, instead of 7-8%; by its longer postdorsal length, usually 51-54% of standard length, instead of 48-51% (dorsal fin about equidistant between snout and caudal base); and importantly, by its nine anal rays, rather than eight. The blunt snout, depigmented caudal base, and tubercle characters by which *N. camurus* was distinguished from *N. whipplei* will also serve for *N. spilopterus,* and in addition, breeding male *N. spilopterus* have moderately large tubercles on the nape and notal ridge, and lack an enlarged dorsal fin.

N. v. venustus may be easily distinguished by the presence of its black caudal spot and eight anal rays, and by its lack of the contrasting black pigment of the posterior dorsal membranes or depigmented caudal base.

Description.—Teeth 1,4-4,1, hooked, the cutting surfaces narrow, concave, and with or without serrations. Anal rays 9, pectoral rays usually 15 or 16. Dorsal fin moderate in size in non-breeding adults, the third principal ray longest, the rays about equal in the depressed fin; origin about equidistant from tip of snout and caudal base.

Exposed portions of lateral scales higher than wide. Lateral-line scales usually 36-38; predorsal circumferential scales 13-2-11, sometimes 15-2-11. It is worthy of note that a small number of collections show a departure from the count of 11 below the lateral line, which is so dominant in most of the species of *Cyprinella*. These collections have a majority of 12 and 13 counts. Caudal peduncle scales 7-2-5. Scales not crowded before dorsal.

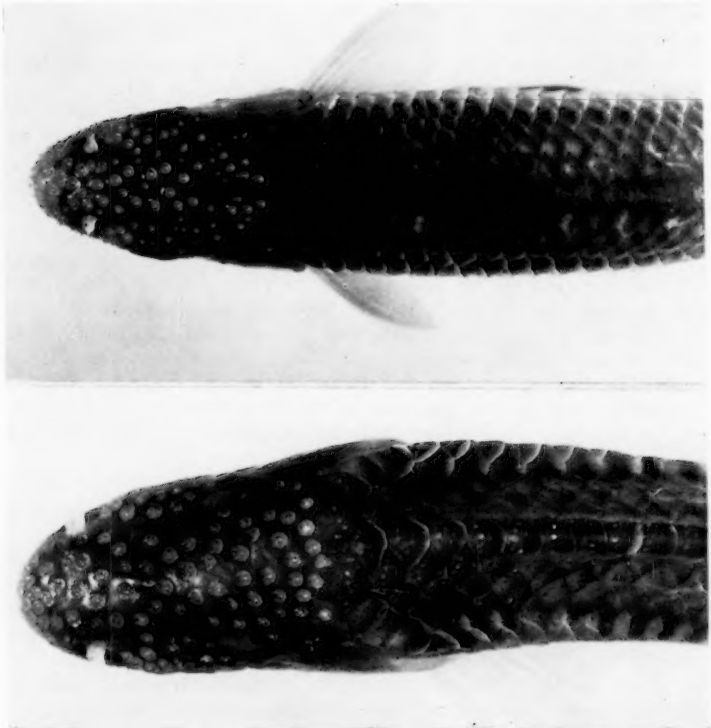


Fig. 2.—Typical breeding tubercle pattern on top of head and back in: (top) *Notropis galacturus* and (bottom) *N. camurus*. The absence of a hiatus between tubercles of snout and those of the top of the head is characteristic of these two species alone among the *Cyprinella*.

Head bluntly triangular. Orbit usually 7-8% of standard length, as long as snout or slightly shorter, 3½-4 in head. Snout quite blunt and rounded. Mouth terminal or subterminal, oblique, moderate in size, upper jaw usually 8-9% of standard length; the upper jaw usually reaches just behind the anterior margin of the orbit and is slightly longer than orbit.

Body moderately deep, usually 24-27% of standard length, somewhat compressed; caudal peduncle depth 11-13% of standard length. Lateral line slightly to moderately decurved from opercular margin to below posterior part of dorsal fin.

Breeding males with tubercles similar to *N. galacturus*. Head, snout and area between eye and snout with concentrations of scattered tubercles; no hiatus between those of head and snout. Two rows on each chin ramus. Nape tubercles very small, becoming almost invisible on the notal ridge before the dorsal fin. Tiny pearl organs over most body scales and on fin rays, following the branchings.

Coloration.—Lateral scales narrowly outlined in black, appearing diamond-shaped. An indistinct lateral stripe present on the posterior half of the body. A poorly-developed dark humeral bar present, extending from opposite upper opercular margin to base of pectoral fin. Dorsum with a narrow stripe before and after the dorsal fin, extending to the procurrent caudal rays. Venter immaculate below a scale row or two under the lateral line.

The depigmentation of the caudal base is not as well defined as it usually is in *N. galacturus*. Commonly it forms a light bar at the base of the caudal rays, flaring slightly dorsally and ventrally. Often it is a shallowly emarginate area, reminiscent of the basicaudal patches of *N. galacturus*.

The dorsal fin is well-pigmented on all its membranes from an early stage, the last two membranes prominently darker than the rest. The caudal fin is lightly pigmented except for the blanched base, and there is sometimes a row of pigment along some of the leading pectoral rays. The pelvics and anal are without melanophores.

Breeding males have red dorsal and caudal fins, and all fins are suffused with milky pigment.

Races.—Two distinct populations of *Notropis camurus* are known, one in tributaries of the Arkansas River, the other in Mississippi River tributaries in Mississippi. Tables I, II, IV indicate that a fairly wide divergence has taken place between these two populations. For example, a line drawn between 36 and 37 lateral-line scales results in an index of divergence of 76.3. A far greater proportion of Arkansas specimens have more than 13 predorsal circumferential scales above the lateral line than do Lower Mississippi fish. In proportional characters, the Lower Mississippi population tends toward a more streamlined form, approaching *N. whipplei*, rather than the straight contours of Arkansas River *N. camurus*. While body depth shows little difference, the caudal peduncle of the Lower Mississippi population tends to be less deep. Dorsal origin-lateral line is somewhat less in the Lower Mississippi forms than in those from the Arkansas, and both eye and upper jaw tend to average larger. By some standards, these two populations might be called subspecies,

TABLE III.—Frequency distribution of body proportions, expressed as per cent of standard length, of *Notropis galacturus* and *N. camurus*

River System	Predorsal length								
	50	51	52	53	54	55	56	57	N
N. galacturus									
White	....	....	8	4	3	....	1	....	16
Tennessee-Cumberland	1	1	1	8	11	12	1	1	36
N. camurus									
Osage	....	....	....	....	1	1	....	....	2
Arkansas	2	6	14	4	1	....	....	....	27
Lower Mississippi	....	2	6	6	4	1	....	....	19

	Postdorsal length									
	46	47	48	49	50	51	52	53	54	N
N. galacturus										
White	....	1	4	5	6	....	....	....	....	16
Tennessee-Cumberland	2	3	12	13	4	2	....	....	....	36
N. camurus										
Osage	....	....	....	....	....	2	....	....	....	2
Arkansas	....	....	....	1	3	9	9	4	1	27
Lower Mississippi	....	....	....	2	5	7	3	2	....	19

TABLE III.—(continued)

River System	Head length						
	23	24	25	26	27	28	N
N. galacturus							
White	1	6	5	4	....	....	16
Tennessee-Cumberland	....	4	14	15	3	....	36
N. camurus							
Osage	....	....	....	1	1	....	2
Arkansas	....	....	2	12	11	2	27
Lower Mississippi	....	....	2	7	6	4	19

	Caudal peduncle depth					
	9	10	11	12	13	N
N. galacturus						
White	2	13	1	....	....	16
Tennessee-Cumberland	1	18	17	....	....	36
N. camurus						
Osage	....	....	....	....	2	2
Arkansas	....	....	....	18	9	27
Lower Mississippi	....	....	8	11	....	19

TABLE IV.—Frequency distribution of body proportions, expressed as per cent of standard length, of *Notropis galacturus* and *N. camurus*

River System	Body depth													Orbit length				
	19	20	21	22	23	24	25	26	27	28	29	30	N	6	7	8	9	N
N. galacturus																		
White	2	4	8	2	....	....	....	....	....	....	....	....	16	2	11	3	....	16
Tennessee-Cumberland	....	1	10	12	10	2	1	....	....	....	....	....	36	2	26	8	....	36
N. camurus																		
Osage	....	....	....	....	....	....	....	....	....	....	....	2	2	....	1	1	....	2
Arkansas	....	....	....	....	....	3	7	10	6	1	....	....	27	....	17	10	....	27
Lower Mississippi	....	....	....	1	....	4	3	6	4	1	....	....	19	....	....	15	4	19

	Dorsal origin				Lateral line					Upper jaw length			
	12	13	14	15	16	17	18	19	N	7	8	9	N
N. galacturus													
White	1	4	10	1	....	....	....	....	16	9	7	....	16
Tennessee-Cumberland	....	2	19	12	2	1	....	....	36	7	27	2	36
N. camurus													
Osage	....	....	....	....	....	....	....	2	2	....	....	2	2
Arkansas	1	....	....	1	2	16	7	....	27	....	11	16	27
Lower Mississippi	....	....	1	3	10	5	....	....	19	....	1	18	19

at least on the basis of the divergence in lateral-line scales. The mode of the Lower Mississippi population, however, overlaps the Arkansas population at a high point in the latter's distribution, so that actual separation would be quite difficult. In this study, therefore, the two populations are considered as races, the *Arkansas Race* and the *Lower Mississippi Race*.

A single sample from the Osage, a tributary of the Missouri River, falls extreme in many proportional characters, but is tentatively included in the Arkansas race. No data are available for the sparse material from the upper White River system, where *N. camurus* occurs with *N. galacturus*.

Range.—Upper Arkansas River and tributaries in Arkansas, Missouri, Oklahoma, Kansas and Colorado. Particularly abundant in the Neosho and Illinois Rivers. Rare in Osage River. Tributaries of the Lower Mississippi River in Mississippi and Louisiana.

Habitat.—Cross (1954: 309) states that the species in Kansas prefers moderately fast, clear water, and its abundance in the two Ozark streams, the Neosho and Illinois Rivers, would seem to bear this out. Moore (*in litt.*) however, has indicated that in the more westerly portions of its distribution, the species is found in warmer, more turbid waters. The habitat of the Lower Mississippi race has been described by Bailey and Taylor (1950: 37) in their discussion of *Noturus* (= *Schilbeodes*) *hildebrandi*. The race appears to favor those high gradient streams with clear waters and sandy bottoms, and probably will not be found in more sluggish, flood-plain tributaries.

Etymology.—The name *camurus* is apparently derived from the Latin *camur*, turned inward, in allusion to the blunt snout.

DISPERSAL AND SPECIATION IN THE COMPLEX

From the close relationship of *N. camurus* and *N. galacturus*, it seems obvious that they were derived from a common stock in the distant past. This stock was presumably divided into eastern and western portions, and the two species evolved (see Fig. 3).

Probably *N. camurus* was at one time far more widely distributed than at present, as indicated by the type locality in eastern Colorado, far west of the nearest recent record, and perhaps by the specimens in the White drainage, which may be remnants of a population which has been unable to meet competition successfully. The presence of the Lower Mississippi race may be evidence of a former occupation of much of the lower Mississippi Valley. It seems that the range of the species is contracting at present, and that the southwestern Ozark region is its stronghold. The precise competitive status of the Lower Mississippi race is too poorly known to permit speculation, but where it is found, the species seems to flourish.

N. galacturus probably differentiated in the Tennessee system, becoming adapted to the cool, mountain waters of the uplands. At a comparatively recent date, possibly when glacial effects brought about the presence of cool connections to the Arkansas, White and St. Francis systems, the species crossed the Mississippi and became established in cooler waters to the west. If it was ever present in the Arkansas, there is no longer any evidence, but it is possible that the

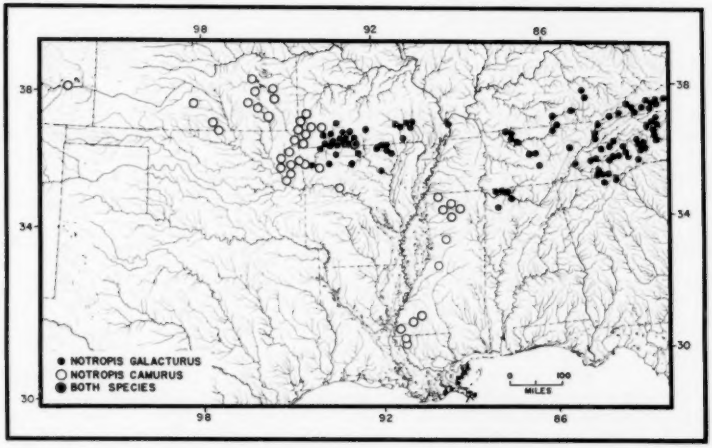


Fig. 3.—Distribution of collections examined of *Notropis galacturus* and *N. camurus*. Records of Ross and Perkins (1959) from the upper Kanawha system are not shown. Dotted line at right marks part of the divide between Tennessee and Atlantic coastal drainages.

warming following the last glacial period has caused a more extensive range to shrink, until it became confined to the faster, cooler portions of the White and St. Francis. That connections may be possible even at present between the populations east and west of the Mississippi is indicated by the collection of *N. galacturus* supposedly taken at Wyatt, Missouri, almost halfway between the two ranges, but much nearer the mouth of the Tennessee than that of the White.

The occurrence of *N. galacturus* in headwater tributaries of the Savannah and Santee systems is doubtless due to stream piracy across the Appalachian divide from Tennessee River tributaries. Ross and Perkins (1959) have recently reported the species from the upper New River in Virginia (Kanawha system). This is apparently due to piracy involving the New and upper Tennessee tributaries, both to the west of the east-west divide.

REFERENCES

BAILEY, REEVE M. AND WILLIAM RALPH TAYLOR 1950. *Schilbeodes hildebrandi*, a new ameiurid catfish from Mississippi. *Copeia*, **1950**(1):31-38.

CALL, R. ELLSWORTH 1893. Memoranda on a collection of fishes from the Ozark region of Missouri. *Proc. Davenport Acad. Sci.*, **5**(1887):73-80.

COCKERELL, T. D. A. 1911. The scales of freshwater fishes. *Biol. Bull.*, **20**: 367-387.

COPE, E. D. 1867. On the genera of fresh-water fishes *Hypsilepis* Baird and *Photogenis* Cope, their species and distribution. *Proc. Acad. Nat. Sci. Phila.*, **19**:156-166.

———1869. On the distribution of fresh-water fishes in the Allegheny region of southwestern Virginia. *J. Acad. Nat. Sci. Phila.*, **6**:207-247.

———1870. A partial synopsis of the fishes of the fresh waters of North Carolina. *Proc. Am. Philos. Soc.*, **11**:448-495.

CRAGIN, F. W. 1885. Preliminary list of Kansas fishes. *Bull. Washburn Lab. Nat. Hist.*, **50**:105-111.

CROSS, FRANK B. 1954. Fishes of Cedar Creek and the South Fork of the Cottonwood River, Chase County, Kansas. *Trans. Kans. Acad. Sci.*, **57**:303-314.

DRIVER, ERNEST C. 1942. Name that animal. Northampton, Mass., Kraushar Press. 527 p.

EVERMANN, BARTON W. 1918. The fishes of Kentucky and Tennessee: a distributional list of the known species. *Bull. U. S. Bur. Fish.*, **35**:293-368.

——— AND SAMUEL F. HILDEBRAND 1916. Notes on the fishes of east Tennessee. *Ibid.*, **34**:431-451.

——— AND WILLIAM C. KENDALL 1895. A list of the species of fishes known from the vicinity of Neosho, Missouri. *Bull. U. S. Fish Comm.*, **14**: 469-472.

FOWLER, HENRY W. 1910. Notes on the variation of some species of the genus *Notropis*. *Proc. Acad. Nat. Sci. Phila.*, **62**:273-293. 7 plates.

———1923. Records of fishes for the southern states. *Proc. Biol. Soc. Wash.*, **36**:7-34.

———1936a. Fresh-water fishes obtained in North Carolina in 1930 and 1934. *Fish Cul.*, **15**:192.

———1936b. Note on some Tennessee fishes, 1930. *Ibid.*, **15**:111.

———1945. A study of the fishes of the southern piedmont and coastal plain. *Acad. Nat. Sci. Phila. Monogr.*, 7. vi + 408 p., 313 figs.

GIBBS, ROBERT H., JR. 1957a. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis* I. Systematic status of the subgenus *Cyprinella*, with a key to the species exclusive of the *lutrensis-ornatus* complex. *Copeia*, **1957**(3): 185-195.

———1957b. *Ibid.* 2. Distribution and variation of *Notropis spilopterus*, with the description of a new subspecies. *Lloydia*, **20**(3):186-211.

———1957c. *Ibid* 3. Variation and subspecies of *Notropis venustus* (Girard). *Tulane Stud. Zool.*, **5**(8):175-203.

GILBERT, CHARLES H. 1886. Third series of notes on Kansas fishes. *Bull. Washburn Lab. Nat. Hist.*, **1**:207-211.

———1889. Fourth series of notes on the fishes of *Kansas*. *Ibid.*, **2**:38-43.

———1891. Report of explorations made in Alabama during 1889, with notes on the fishes of Tennessee, Alabama, and Escambia rivers. *Bull. U. S. Fish Comm.*, **9**:143-159.

GOLDSBOROUGH, EDMUND LEE AND HOWARD WALTON CLARK 1908. Fishes of West Virginia. *Bull. U. S. Bur. Fish.*, **27**:29-39.

GRAHAM, I. D. 1885. Preliminary list of Kansas fishes. *Trans. Kans. Acad. Sci.*, **9**:69-78.

GUNTHER, ALBERT 1868. Catalogue of the fishes in the British Museum. Vol. 7. xx + 512 p.

HILDEBRAND, SAMUEL F. 1932. On a collection of fishes from the Tuckasegee and upper Catawba river basins, N. C., with a description of a new darter. *J. Elisha Mitchell Sci. Soc.*, **48**:50-82.

HUBBS, CARL L. AND KARL F. LAGLER 1958. Fishes of the Great Lakes region. *Cranbrook Inst. Sci. Bull.*, **26**. xi + 213 p.

JORDAN, DAVID S. 1877. A partial synopsis of the fishes of upper Georgia. *Ann. N. Y. Lyceum Nat. Hist.*, **11**:307-377.

———1878a. Manual of the vertebrates of the northern United States. Ed. 2. Chicago. Jansen, McClurg and Co. 407 p.

———1878b. A catalogue of the fishes of the fresh waters of North America. *Bull. U. S. Geol. and Geogr. Surv. Terr.*, **4**:407-442.

———1879. On the distribution of fresh-water fishes of the United States. *Ann. N. Y. Acad. Sci.*, **1**:92-120.

———1880. Manual of the vertebrates of the northern United States. Ed. 3. Chicago. Jansen, McClurg and Co. 406 p.

———1884. *Ibid.* Ed. 4. 406 p.

———1885. A catalogue of the fishes known to inhabit the waters of North America, north of the tropic of cancer, with notes on the species discovered in 1883 and 1884. Rep. U. S. Comm. Fish and Fish., 1885:789-793.

———1889. Report of explorations made during 1888 in the Allegheny region of Virginia, North Carolina, and Tennessee, and in western Indiana, with an account of the fishes found in each of the river basins of those regions. *Bull. U. S. Fish. Comm.*, **8**:97-173.

———1891. Report of explorations in Colorado and Utah during the summer of 1889, with an account of the fishes found in each of the river basins examined. *Ibid.*, **9**:1-40.

———1899. A manual of the vertebrate animals of the northern United States. Ed. 8. Chicago. A. C. McClurg and Co. vi + 397 p.

———1910. *Ibid.* Ed. 10. vi + 397 p.

———1916. *Ibid.* Ed. 12. vi + 397 p.

——— AND ALEMBERT W. BRAYTON 1878. On the distribution of the fishes of the Allegheny region of South Carolina, Georgia, and Tennessee, with descriptions of new or little known species. Contr. to N. Amer. Ichthy. 3. *U. S. Nat. Mus. Bull.*, **12**:1-95.

——— AND HERBERT E. COPELAND 1876. Check list of the fishes of the fresh waters of North America. *Bull. Buffalo Soc. Nat. Hist.*, **3**:133-164.

——— AND BARTON W. EVERMANN 1896a. The fishes of North and Middle America. U. S. Nat. Mus. Bull. 47. Part 1. lx + 1240 p.

——— AND ———1896b. A checklist of the fishes and fish-like vertebrates of North and Middle America. Rep. Comm. Fish and Fish. 1895. Part 2: 207-590.

———, ——— AND HOWARD WALTON CLARK 1930. Check list of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rep. U. S. Comm. Fish. 1928. Part 2:1-670.

——— AND CHARLES H. GILBERT 1883. Synopsis of the fishes of North America. *U. S. Nat. Mus. Bull.*, **16**:lvi + 1018 p.

——— AND ———1887. List of fishes collected in Arkansas, Indian Territory, and Texas, in September, 1884, with notes and descriptions. *Proc. U. S. Nat. Mus.*, **9**:1-25.

——— AND SETH E. MEEK 1885. Description of four new species of Cyprinidae in the United States National Museum. *Ibid.*, **7**:474-477.

KIRSCH, PHILIP H. 1892. Notes on the streams and fishes of Clinton County, Kentucky, with a description of a new darter. *Bull. U. S. Fish Comm.*, **10**:289-292.

———1893. Notes on a collection of fishes from the southern tributaries of the Cumberland River in Kentucky and Tennessee. *Ibid.*, **11**:259-268.

KUHNE, EUGENE R. 1939. A guide to the fishes of Tennessee and the mid-south. Tenn. Dept. of Conserv. 124 p.

MEEK, SETH E. 1891. Report of the explorations made in Missouri and Arkansas during 1889, with an account of the fishes observed in each of the river basins examined. *Bull. U. S. Fish Comm.*, **9**:113-141.

———1895. Report of investigations respecting the fishes of Arkansas conducted during 1891, 1892, and 1893, with a synopsis of previous explorations in the same state. *Ibid.*, **14**:67-94.

MOORE, GEORGE A. 1952. Fishes of Oklahoma. Okla. Game and Fish Dept.

——— AND JOHN M. PADEN 1950. The fishes of the Illinois River in Oklahoma and Arkansas. *Am. Midl. Nat.*, **44**:76-95.

PICKENS, A. L. 1928. Fishes of upper South Carolina. *Copeia*, No. **167**:29-32.

PRATT, HENRY SHERRING 1923. A manual of the land and fresh water vertebrate animals of the United States. Philadelphia. P. Blakiston's Son and Co. xv + 422 p.

———1935. *Ibid.* Rev. Ed. xvii + 416 p.

ROSS, ROBERT D. 1959. Drainage evolution and distribution problems of the fishes of the New (Upper Kanawha) River system in Virginia. Part IV. Key to the identification of fishes. *Va. Agr. Exper. Sta. Techn. Bull.*, **146**:1-27.

——— AND BENJAMIN D. PERKINS 1959. *Ibid.* Part III. Records of fishes of the New River. *Techn. Bull.*, **145**:1-35.

SCHRENKEISEN, RAY 1938. Field book of fresh-water fishes of North America north of Mexico. New York. G. P. Putnam's Sons. xii +312 p.

SHOUP, C. S. AND S. H. PEYTON 1940. Collections from the drainage of the Big South Fork of the Cumberland River in Tennessee. *Rep. Reelfoot Lake Biol. Sta.*, **4**:106-116.

———, ——— AND GLENN GENTRY 1941. A limited biological survey of the Obey River and adjacent streams in Tennessee. *Ibid.*, **5**:48-76.

SMITH, HUGH M. 1907. The fishes of North Carolina. N. C. Geol. and Econ. Surv. Vol. 2. xi + 453 p.

WOOLMAN, ALBERT J. 1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained. *Bull. U. S. Fish Comm.*, **10**: 249-288.

Mycological Notes II.[1] New Taxa, Synonyms, and Records[2]

MARIE L. FARR

Crops Research Division, Agricultural Research Service, United States Department of Agriculture Beltsville, Maryland

ABSTRACT: The following items are included in this paper: 1) Three specimens of *Perichaena microspora* Penz. & List. ap. Penz. from the southern U. S. are discussed and the specific description is amended. This apparently represents the first published record of this species for the western hemisphere. (2) *Lojkania cynodonifolii* [sic] Bat. is relegated to synonomy under *Dimeriella erysipheoides* (Ell. & Ev.) Farr. The reasons for this step, as well as some details explaining the taxonomic background of *Dimeriella erysipheoides*, are presented. 3) The following new fungi are described: *Corynespora elaeidicola* Ell. var. *cercosporioides* Farr on *Heliconia curtispatha* Ped. leaves from Panama; *Peltaster intermedius* Farr on *Ananas comosus* (L.) Merr. leaves from Cambodia; and *Didymella minuta* Farr on *Sesamum indicum* L. leaves from Cambodia. 4) *Cylindrosporium sesami* Hansf., causing a leaf spot disease on sesame, is reported, apparently for the first time, from Asia. 5) New localities, both in Asia, are given for two species of *Cercospora*, *C. melastomobia* Yam. and *C. helianthicola* Chupp and Viég.

PERICHAENA MICROSPORA IN THE WESTERN HEMISPHERE

Perichaena microspora Penz. & List. ap. Penz. was described from Java and Ceylon (Penzig, 1898) and, if included in a major monograph (Lister, 1925; Macbride and Martin, 1934; Hagelstein, 1944), is listed only from these two localities. In a recent publication (Farr, 1959) this species was reported from Africa. (The African collection, gathered by O. F. Cook in Liberia in 1894, is actually four years older than the type specimen, but apparently was overlooked or neglected until 1959.)

At the annual foray of the Mycological Society of America in August, 1960, *Perichaena microspora* was found in Louisiana by George W. Martin and by me. The two specimens were independently collected in the same locality, West Feliciana Parish, Audubon State Park, and each consisted of several small plasmodiocarps on dead needles of *Pinus taeda* L.

---

[1] The first article of this series appeared in Mycopathologia et Mycologia Applicata 12:283-288. 25 May, 1960.

[2] My thanks are due to C. R. Benjamin and J. A. Stevenson for constructive criticism regarding the manuscript; G. W. Martin for contributing slides of *Perichaena microspora* and helpful comments about this species; C. G. Shaw for the loan of *Lojkania cynodonifolii* type material; R. G. Orellana for providing named herbarium material and cultures of *Cylindrosporium sesami;* and E. K. Cash for checking the Latin diagnoses.

These gatherings were initially believed to represent the first finds of this species in the western hemisphere, but recently Professor Martin unearthed an earlier collection made by Dr. Erdman West near Gainesville, Florida, in July, 1950, and deposited in part in the herbarium of the State University of Iowa. A slide of this material is in the National Fungus Collections. Dr. West did not publish on this collection and has kindly given me permission to do so in this note.

The Louisiana specimens are deposited in the herbaria of the State University of Iowa (SUI) and the National Fungus Collections (NFC) respectively. The latter specimen (NFC no. *71645*) is the only collection I saw in habit and it agrees in external (as well as microscopic) characteristics with the diagnosis and Lister's excellent illustration (1925, pl. 185). The capillitium is studded with delicate spines and in part prominently constricted at regular intervals so as to give a beaded appearance under oil immersion. The non-beaded portions display frequent irregular expansions and a consequently fluctuating diameter of 1.5-5 (mostly 2-3.5) μ (Fig. 1). Professor Martin reports fine ridges present in addition to the spines in parts of his material (personal communication). These ridges could also be seen in the Florida specimen. The capillitium of the latter, densely covered with spines to 2μ long, is hardly at all constricted and has a nearly uniform diameter of ca. 2μ, sometimes conspicuously swollen at the axils.

The description furnished by Lister (1925), though otherwise excellent, is rather limited with respect to the capillitium. It depicts the latter as "marked with minute spines, regularly constricted at intervals of 1 to 2 μ." Petch (1910: 369) mentions, in addition, "frequent irregular expansions at the axils," and also refers to the beaded appearance of the threads. These descriptions, however, are now somewhat inadequate, since they fail to include certain variations encountered in the American fruitings. In order to present a more complete picture it seems desirable, therefore, to emend that part of the species description dealing with the capillitium, as follows:

> capillitium a loose network of branching threads, yellowish-pink in mass, almost colorless when mounted, densely covered with delicate spines up to 2μ long, and sometimes in part with fine ridges; threads almost even to torulose, of a nearly uniform diameter of 1.5-2μ and with nodular enlargements at the axils, or sometimes of irregular diameter (1.5-5μ) throughout.

The spores of all three collections are minutely spinulose and measure 6.5-8.5μ diam.

Although *P. microspora* is brightly colored and not one of the most minute Myxomycetes, its elusiveness is understandable. The scattered fructifications are more or less buried in forest litter and thus frequently concealed from the collector's view. A more intense search may reveal the species to be more common and of wider distribution than we believe it to be at present.

LOJKANIA CYNODONIFOLII [SIC] BATISTA, A SYNONYM

Recently (1960) Batista described a new species of the previously monotypic genus *Lojkania* Rehm, *L. cynodonifolii* Bat., ap. Bat. & Peres. The type of this species, labelled "*Dimerosporium erysipheoides* Ell. and Ev.", was collected on *Cynodon dactylon* (L.) Pers. by B. C. Tharp at Texarkana, Texas, 16 October, 1915. It is deposited in the herbarium of the State University of Washington.

At nearly the same time as Batista's publication, I published the new combination *Dimeriella erysipheoides* (Ell. & Ev.) Farr based on type material of *Dimerosporium erysipheoides* Ell. & Ev. and a Cambodian collection on the same host (Farr, 1960).

The genus *Dimerosporium* Fckl. is no longer valid since its type, *D. abjectum* (Wallr.) Fckl. is a synonym of *Asterina veronicae* (Lib.) Cke. (Stevens and Ryan, 1939:50). The type of *Dimerosporium erysipheoides,* however, was found to be not an *Asterina,* but rather to represent a distinct species of the genus *Dimeriella* Speg. (Meliolaceae or Sphaeriaceae) and hence was transferred there. Spegazzini (1908:12) segregated *Dimeriella* from *Dimerosporium* by the following statement: "Genus e *Dimerosporio* excerptum, species peritheciis subglobosis astomis setulosis sporis hyalinis donatas sistens."

The genus *Lojkania,* described by Rehm in 1905, apparently differs from *Dimeriella* chiefly in having dark spores and glabrous perithecia. In Batista's description and illustration the spores of *Lojkania cynodonifolii* are olivaceous-brown and the perithecia glabrous, but careful scrutiny of his type specimen reveals a few scattered appendages on the perithecia; the spores, furthermore, at maturity are not brown. Their subhyaline to greenish color appears to be due to the densely granular contents. The perithecial appendages are scarce and sometimes poorly developed, and hence very inconspicuous. The well-formed ones are dark brown and wider than the hyphae, with a more or less bilobed apex. Except for being less numerous, the setae correspond well with those of Ellis and Everhart's (1888) diagnosis of *Dimerosporium erysipheoides,* which reads "[perithecia] surrounded below with 15-20 short spreading appendages 30-40 × 3, mostly 1-3-septate, brown and imperfectly bilobate at their extremities." They also appear identical with those of the Cambodian material. The measurements as well as the habit and macroscopic appearance of the Ellis and Everhart type, the Cambodian specimen, and Batista's type of *Lojkania cynodonifolii* agree closely. Thus it can be reasonably asserted that all the material cited and discussed above is of one and the same species and belongs in the genus *Dimeriella. Lojkania cynodonifolii* Batista, therefore, becomes a synonym of *Dimeriella erysipheoides* (Ell. & Ev.) Farr.

CORYNESPORA ON HELICONIA

A collection of leaves of *Heliconia curtispatha* Petersen from Panama was found to be infected with a species of *Corynespora*

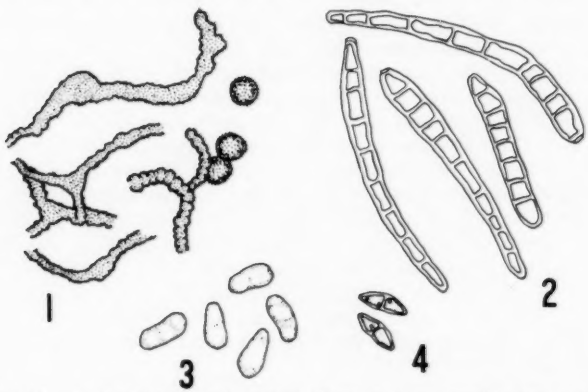
Güssow (Dematiaceae). This fungus genus has apparently not previously been reported from the Musaceae. The fungus is widely distributed over extensive light brown blotches which, on the upper leaf surface, have a dark brown border and are sometimes surrounded by a bright yellow halo. Whether the *Corynespora* causes the spots or is merely a secondary invader cannot be established at this time.

This hyphomycete strongly suggests a *Cercospora* because of its narrow conidia, but their general shape and the greater prominence of the walls seem more characteristic of *Corynespora*. The organism appears to be on the border line between the two genera. Other particulars of this fungus include the presence of light to dark brown stromata; nearly straight to strongly geniculate, fascicled conidiophores mostly between 105μ and 275μ long and 3-5μ in diameter; and pale brown, sometimes guttulate conidia measuring 40-85μ (av. 67) in length and 5-7μ(8) in width. It comports with the description and illustration of *Corynespora elaeidicola* Ellis (1960:24, Fig. 16) in all respects except in the possession of much longer conidiophores and large numbers of conidia that are attenuated rather than blunt at the apex, as shown in Ellis' drawing; furthermore, *C. elaeidicola* so far has been reported only on the Palmaceae. The fungus on the *Heliconia* is therefore described here as a variety of *Corynespora elaeidicola*.

Corynespora elaeidicola Ellis var. ***cercosporioides*** var. nov.
Fig. 2

A typo differt conidiophoris longis, conidiis ad apicem saepe attenuatis.

Type.—On leaves of *Heliconia curtispatha* Petersen, Canal Zone, Panama; ex E. P. Imle s.n., Dec. 1959. (NFC 71646).



Figs. 1-4—1. *Perichaena microspora* Penz. & List., capillitium and spores; ×500. (NFC 71645). 2. *Corynespora elaeidicola* Ellis var. *cercosporioides* Farr, spores; ×620. (Type). 3. *Peltaster intermedius* Farr, spores ×600. (Type). 4. *Didymella minuta* Farr, ×635. (Type).

A NEW SPECIES OF PELTASTER

Two specimens of pineapple leaves received from Cambodia exhibited a superficial black mold with mycelium resembling that of *Asterinella stuhlmanni* (P. Henn.) Theiss. and possibly belonging to the conidial state of the same. Since, however, no ascogenous fruit bodies were present and apparently no pycnidial state is known for the *Asterinella*, the fungus on the Cambodian material is here described as a new species of *Peltaster* (Leptostromataceae).

A tabular comparison (Table I) of this fungus with the three previously described species of *Peltaster* (*P. hedyotidis* Sydow, 1917: 261; *P. guraniae* Toro ap. Chardon and Toro, 1934:232; and *P. byrsonimae Hansford*, 1955:83) shows that the conidia of the new

TABLE I.—A comparison of the species of *Peltaster*

Species	Diameter of fruit bodies	Size of spores	Habit
P. Hedyotidis Syd.	110-150μ	8-10 × 4-5μ	hypophyllous
P. byrsonimae Hansf.	to 180μ	14-17 × 3-3.5μ	hypophyllous
P. guraniae Toro ap. Chardon & Toro	331-486 × 57-80μ	6-9 × 2-3μ	hypophyllous
P. intermedius sp. nov.	150-220μ	10-13 × 5μ	epiphyllous or hypophyllous

species are wider than those of all other species except *P. hedyotidis*, but the range of their length falls between that of *P. hedyotidis* and that of the other two species. The fruit bodies are larger than those of *P. hedyotidis*, smaller and of a different shape than those of *P. guraniae*, and apparently overlapping those of *P. byrsonimae* in diameter. The new species is, furthermore, the only one so far reported on a monocot.

Peltaster intermedius sp. nov.
Fig. 3

Mycelium ex hyphis sinuoso-reticulatis, ramosis, exhyphopodiatis, olivaceis vel atro-brunneis, indistincte septatis, 2-4μ diam. compositum; pycnidia singula vel connata, in hyphis mycelii evoluta, 150-220μ diam., orbiculata, scutata, poro centrali vel eccentrali dehiscens; paries superior radiatus, margine plus minusve fimbriatus, ex hyphis brunneis compositus; conidia hyalina, continua, 1-3-guttulata, oblonga vel elliptica, 10-13 × 5μ, utrinque rotundata.

Mycelium superficial, wavy-reticulate, branching, generally asterinaceous in appearance but without hyphopodia, olivaceous to deep brown, darkest near the fruit bodies or fruit body initials, indistinctly septate, 2-4μ diam.; pycnidia single or several fused, 150-220μ diam., covered by a network of mycelium, orbicular, scutate, dark brown with a more or less fimbriate margin and a cen-

tral or eccentric pore; conidia hyaline, continuous, 1-3-guttulate, 10-13 × 5μ, oblong to elliptical, sometimes shoe-shaped, the ends rounded.

Holotype.—On leaves of *Ananas comosus* (L.) Merr., Chamcar Krauch, Cambodia, *Litzenberger 314,* 30 Oct. 1959. (NFC 71647).

Paratype.—On the same host from the same locality, *Litzenberger 60,* 27 Aug. 1958. (NFC 71648).

A number of the conidia, when mounted in lactophenol, appeared one- or two-septate, but examination under oil immersion indicated that this was due to the arrangement of the droplets which are sometimes very close together and separated only by a thin strand of cytoplasm. In an aqueous phloxine mount, the droplets remain unstained, but are not as sharply delimited as in lactophenol.

DIDYMELLA ON SESAME

A minute species of *Didymella* (Sphaeriaceae or Pleosporaceae) was found scattered on some leaf spots of two *Sesamum indicum* L. specimens from Cambodia. The spots were of irregular shape, pale brown with concentric lines and dark brown borders, and resembled those caused by *Alternaria* sp. Dematiaceous conidiophores and several types of detached dematiaceous spores were descernible on the leaf surface. Whether the *Didymella* was parasitic or saprophytic could not be ascertained from the material and information on hand; possibly it represented the perfect stage associated with one of the Dematiaceae.

Evidently no members of the genus *Didymella* have been reported from any species of the Pedaliaceae. The organism on the sesame leaves varies from most *Didymella* reported from dead leaves of various plants primarily in its conspicuously small perithecia. From *D. exigua* (Niessl) Sacc. and *D. pedicularidis* v. Arx, with both of which it essentially agrees in perithecial, ascus, and ascospore measurements, it differs in its non-constricted ascospores.[3] The perithecial wall cells of *D. exigua,* furthermore, are "at times roughened by scattered thick-walled, protruding cells, tomentose" (Barr, 1959) while those of the sesame fungus appear consistently thin and smooth. The latter is therefore described as a new species.

Didymella minuta sp. nov.
Fig. 4

Perithecia erumpentia, nigra, membranacea, globosa, ostiolata, c. 70-90μ diam.; asci cylindracei vel elliptici, 8-spori, bitunicati, 40-50 × 10-13μ; paraphyses filiformes; ascosporae 1-septatae, hyalinae, fusiformae, rectae vel leniter curvatae, non vel vix constrictae, guttulatae, 11-15 × 3-4.5μ.

Perithecia erumpent, black, membranous, globose, ostiolate, c. 70-90μ diam.

[3] Barr (1959) describes the ascospores of *D. pedicularidis* as not constricted. V. Arx (1950), on the other hand, states that they are more or less constricted; in his sketch they appear definitely constricted, and not so pronouncedly fusiform as those of the sesame fungus.

at maturity; ostiole a roundish pore, c. 20μ diam.; perithecial wall composed of smooth, variously-shaped cells 5-8μ diam., those around the ostiole often being darker; asci cylindrical or elliptical, 8-spored, bitunicate, 40-50 x 10-13μ; paraphyses filiform; ascospores 1-septate, greenish-hyaline, spindle-shaped, straight or slightly curved, not or scarcely constricted at the septum, guttulate, 11-15 x 3-4.5μ.

Holotype.—On leaves of *Sesamum indicum* L., Kompong Cham, Cambodia, *Litzenberger 12,* 1958. (NFC 71649).

Paratype.—On same host, Reilin, Cambodia, *Litzenberger 324,* 1959. (NFC 71650).

CYLINDROSPORIUM SESAMI HANSFORD FROM CAMBODIA

This fungus was described as the causal organism of a leaf spot disease on *Sesamum indicum* L. in Uganda (Hansford, 1938, p. 47). Recently this fungus was noted for the first time in the United States (Anonymous, 1960; Orellana, 1961).

The same organism has now been found on sesame leaves from Cambodia (Prek Leap Sta., *Litzenberger 13,* 10 July 1958. NFC 71651) and the present note apparently constitutes the first report from Asia. The possibility exists, however, that an earlier report of "*Cercosporella* sp." from Malaya (Thompson and Johnston, 1953:29) may refer to the same fungus.

The Cambodian collection agrees well in its measurements with those stated in the species diagnosis of *Cylindrosporium sesami;* it also is identical in microscopic features and in shape of the leaf spots with named American material of this species. The color of the spots differs, however, in being a uniform, opaque gray-brown in the Cambodian material, and a more translucent light-brown in the American specimen. This may be due to a possible association with *Alternaria* sp. (The Cambodian specimen was labelled "Alternaria leaf spot," but only an abundance of the *Cylindrosporium* was detected on the dry leaves.)

NEW LOCALITY RECORDS FOR TWO SPECIES OF CERCOSPORA

Cercospora melastomobia Yamamoto and *C. helianthicola* Chupp & Viégas were listed by Chupp (1953) as known only from their type localities (Formosa and Brazil, respectively) and I could find no additional record of either species in subsequent literature.

C. melastomobia was found on leaves of *Melastoma candidum* D. Don. from Hong King Island, *N.L.H. Krauss 344* and probably *345* (the latter poor material), 30 Apr. 1958. (NFC 71652 and 71653.) The fungus on the former specimen corresponds well with type material of the species.

Some dried leaves of *Helianthus annuus* L. from Cambodia (Siemreap, *Litzenberger 377,* 18 Aug. 1960. NFC 71654) were infected with *Cercospora helianthicola.* In Chupp's monograph, this species is distinguished from the other Cercosporae on *Helianthus* by the

possession of hyaline, acicular conidia; and the Cambodian material is in close agreement with the characterization and illustration of *C. helianthicola.*

The type specimens of the new taxa described in this paper are deposited in the National Fungus Collections, Plant Industry Station, Beltsville, Maryland (NFC).

REFERENCES

ANONYMOUS 1960. *Agrisearch Notes,* **9**(3):15.

ARX, J. A. VON 1950. Einige neue Ascomyceten aus der Schweiz. *Sydowia,* **4**:389. fig. 73.

BARR, M. E. 1959. Northern Pyrenomycetes. I. *Contr. Inst. Bot. Univ. Montreal,* No. 73. 100 p. 142 figs.

BATISTA, A. C. AND G. E. P. PERES 1960. Duas novas espécies de *Lojkania. Saccardoa,* No. 1, p. 31. fig. 1.

CHARDON, C. E. AND R. A. TORO 1934. Mycological Explorations of Venezuela. *Monogr. Univ. Puerto Rico,* ser. B, no. 2,353 p., 33 pls. (1 col.). Rio Piedras, P. R.

CHUPP, C. 1953. A Monograph of *Cercospora.* 667 p., 222 figs., Ithaca, N. Y.

ELLIS, J. B. AND B. M. EVERHART 1888. New species of fungi from various localities. *J. Mycol.,* **4**(12):121.

ELLIS, M. B. 1960. Dematiaceous Hyphomycetes: 1. *C. M. I. Mycol. Pap.,* No. 76, 36 p., 22 figs.

FARR, M. L. 1959. O. F. Cook's myxomycete collection from Liberia and the Canary Islands. *Lloydia,* **22**:295-301.

———1960. Mycological Notes. New species, combinations, and host records. *Mycopath. et Mycol. Appl.,* **12**:284-288.

HAGELSTEIN, R. 1944. *The Mycetozoa of North America.* 306 p., 16 pls. (4 col.), publ. by the author, Mineola, N.Y.

HANSFORD, C. G. 1938. Annual Report of the Plant Pathologist, 1936. *Ann. Rept. Uganda Prot.* (1937), pt. 2, p. 43-50.

———, 1955. Tropical Fungi — V. *Sydowia,* **9**:1-88.

LISTER, A. 1925. *A Monograph of the Mycetozoa.* ed. 3 (revised by G. LISTER, xxxii + 296 p., 60 figs., 222 pls. (many col.).

MACBRIDE, T. H., AND G. W. MARTIN 1934. *The Myxomycetes.* IX + 339 p., 21 pls.

ORELLANA, R. B. 1961. Leaf Spot of Sesame caused by *Cylindrosporium sesami. Phytopath.* 51:89-92, figs. 1, 2.

PENZIG, O. 1898. Die Myxomyceten der Flora von Buitenzorg. 83 p. Leiden, Neth.

PETCH, T. 1910. A list of the Mycetozoa of Ceylon. *Ann. Roy. Bot. Gard., Peradeniya* **4**:309-371.

REHM, H. 1905. Contributiones Mycologicae ad Floram Hungariae. *Növ. Közlem.,* 4:2.

SPEGAZZINI, C. 1908. Fungi Aliquot Paulistani. *Rev. Mus. La Plata,* **15** (2d ser. 2): 7-48.

STEVENS, F. L. AND M. H. RYAN 1939. The Microthyriaceae. *Ill. Biol. Mon.* **17**(2):1-138.

SYDOW, H. AND P. SYDOW 1917. Beitrag zur Kenntnis der Pilzflora der Philippinen-Inseln. *Ann. Myc.,* **15**:165-268.

THOMPSON, A., AND A. JOHNSTON 1953. A host list of plant diseases in Malaya. *C.M.I. Mycol. Pap.,* No. 52. 38 p.

Studies on the Biology of Philophthalmus gralli Mathis and Leger, 1910 (Trematoda: Digenea)[1]

A. FRED WEST

Department of Biological Sciences, Purdue University, Lafayette, Indiana

ABSTRACT: The adult of *Philophthalmus gralli* occurs in the orbit of wild birds and has been obtained experimentally in chicks. Rodents were refractory to infection by the oral route. *Goniobasis* spp. and *Pleurocera acuta* serve as molluscan hosts. The miracidium penetrates the snail only far enough to release a single redia. It localizes in the heart and produces daughter rediae which migrate to the digestive gland and produce megalurous cercariae. Cercariae escape and encyst on the exoskeleton of arthropods which are eaten by the definitive host, in which the worms migrate to the eye by way of the nasolacrimal duct. Factors concerned with such migration are considered and all stages in the life history are described. The family Ommatobrephidae is reduced to synonymy with the Philophthalmidae and the species *Philophthalmus nyrocae* to synonymy with *Philophthalmus gralli.*

Studies on the life histories of digenetic trematodes has yielded information that is basic to the interpretation of affinities between families and more inclusive taxa (La Rue, 1957). The development of the cercarial stage and its type have been particularly useful in postulating relationships that may not be readily apparent from morphology of the adult alone. Such studies have shown that each family has a common cercarial type and that when the life history of one species is determined, that of other cercariae of the same type may be expected to follow a similar pattern.

In his monographic study, Sewell (1922) followed Cort (1915) in recognizing a Megalura Group of cercariae based on the American fresh water species, *Cercaria megalura.* After Stunkard and Cable (1932) found that a very similar marine species was the larva of *Parorchis acanthus,* a cloacal parasite of birds, their procedure was used in this laboratory 25 years ago in attempts to determine the life history of a fresh water species. Although metacercariae were fed to a variety of vertebrates, the adult was not found for a reason that is now apparent: failure to examine the ocular orbit. The clue to that oversight came much later in this laboratory when Cable, Connor and Balling (1960) decided that Travassos (1918) probably was correct in placing *Parorchis* and *Philophthalmus* in a separate family, the Philophthalmidae, rather than in the Echinostomatidae of which those genera were generally regarded to be aberrant representatives. It fol-

[1] Based on a thesis prepared under the direction of Prof. R. M. Cable and submitted in partial fulfillment of the requirements for the Ph.D. degree, Purdue University. I am especially indebted to my colleague, Frank M. Fisher, Jr., who shared in the early phases of this study and later aided in the collection of naturally infected mollusks and birds.

lowed then that the adult of the fresh water cercaria might be a species of *Philophthalmus* occurring in the orbit of birds. Such proved to be the case and preliminary studies were reported in a brief note (Fisher and West, 1958). The present paper reports the life history of the parasite in detail and certain other aspects of its biology.

METHODS

Two species of naturally infected snails were used as a source of larval trematodes: *Goniobasis* sp. from Fourteen Mile Creek in southern Indiana and *Pleurocera acuta* from the Tippecanoe River near Battle Ground, Indiana. Infected snails were detected by isolation in finger bowls of water and maintained for periods of several months in tanks of shallow, well-aerated water containing a thin layer of silt. Small amounts of 10-52-17 fertilizer were added to promote growth of diatoms and other organisms essential to nutrition of the snails. Such growth was further stimulated by 15-16 hours of artificial light per day and by maintaining a water temperature of 25°-30° C with the aid of immersion heaters.

To obtain metacercariae for feeding experiments, infected snails were isolated in finger bowls of water until cercariae emerged and encysted on the glass. The cysts were then scraped loose and fed to chicks, hamsters, rats, mice, guinea pigs and rabbits which were either sacrificed to study migration of the young worms or, if susceptible to infection, maintained as a source of adults. Although miracidia can be obtained in washings from the orbit of infected birds, adult worms usually were removed with a pipette and placed in water or 0.45% NaCl in which eggs were laid in large numbers. Thereafter, the worms were returned to the orbit of the host to be used again if needed. The eggs hatched in a short time and the miracidia were used to study their morphology or for infecting snails which were placed in small stender dishes of water to which various numbers of miracidia were added. Following exposure, the snails were handled as described above for naturally infected ones; some were examined at intervals to observe larval development and others isolated periodically until cercariae emerged.

All stages of the parasite were studied alive in sealed preparations and as whole mounts after fixation in A.F.A. or Bouin's fluid and staining with Semichon's carmine or Harris' hematoxylin. In addition, the silver nitrate technic of Lynch (1933) was used with all stages. Serial sections were prepared after fixation in hot Bouin's fluid and were stained with Harris' hematoxylin and eosin. Unless otherwise stated, drawings were made by microprojection with details added freehand. All measurements are in millimeters unless otherwise idicated.

Worms maintained in vitro were incubated at 38° C in a medium consisting of one part fresh egg albumin, two parts Tyrode's balanced salt solution, three parts distilled water, two drops fresh egg yolk, 200 units/ml. Penicillin-G potassium and 1 mg/ml streptomycin sulfate.

Methods used to investigate possible factors influencing migration in the definitive host are described with the results of such experiments.

OBSERVATIONS AND DISCUSSION

EXPERIMENTAL DETERMINATION OF THE LIFE HISTORY

The first part of the life history was demonstrated experimentally by rearing the adult parasite in the orbit of chickens which were fed metacercariae. The cercariae were from naturally infected snails. The larvae normally encyst on the exoskeleton of arthropods, especially crayfishes, but cysts used in infection experiments were scraped from finger bowls. Many of the worms probably were injured in that process because some chickens did not become infected and others harbored fewer worms than the number of metacercariae fed. It is also likely that some of those that were not injured failed to reach the orbit for other reasons. The largest number of worms found in a naturally infected bird was 20 in a green heron, *Butorides virescens;* they were of various ages to judge from their sizes in contrast to the usually very uniform size of worms from chickens fed a single lot of metacercariae.

The life history was further elucidated experimentally by infecting snails with miracidia from worms reared in chicks. Many snails were thus exposed and sacrificed at intervals to study larval development of the parasite, but 15 *Goniobasis* sp. and 10 *Pleurocera acuta* were maintained and examined periodically for emerging cercariae. Six *P. acuta* survived and 3 shed cercariae at the end of 4 months. When *Goniobasis* sp. did not do so by the end of the 6th month, the 3 surviving individuals were sacrificed; one contained daughter rediae and a few apparently mature cercariae.

Because it is difficult to maintain prosobranch snails in a state of good nutrition in the laboratory, it is possible that under more favorable conditions, infected snails might shed cercariae within less time. Furthermore, it may be that the larger body of *P. acuta* favors the development of rediae and cercariae over the smaller *Goniobasis* sp. which, in natural infections, shed much smaller numbers of cercariae than did *P. acuta.*

Experimental demonstration of the life history was completed by permitting cercariae from experimentally infected *P. acuta* to encyst and feeding the metacercariae back to a chicken which had provided miracidia used to infect the snails, thus obtaining adult worms for the 2nd time from a single host.

TAXONOMY

Dawes (1956) included in the Philophthalmidae the genera *Philophthalmus* and *Pygorchis* but not *Parorchis* and *Echinostephilla* which he treated as isolated genera of the Echinostomatidae. Yamaguti (1958) recognized the Philophthalmidae to include the subfamilies Parorchinae Lal, 1936, Philophthalminae Looss, 1899, and

three new ones: Cloacitrematinae, Echinostephillinae and Skrjabinovermiinae. Not only does each of the new subfamilies contain a single genus but, as Ching (1960) pointed out, *Skrjabinovermis* is a synonym of *Echinostephilla* according to the Zoological Record for 1953. Recently, Dubois and Mahon (1959) transferred the genus *Parorchis* to the family Ommatobrephidae Poche, 1926, which previously had contained only the genotype. A comparison of *Ommatobrephus* with philophthalmid genera reveals no differences that justify recognition of the Ommatobrephidae. That family accordingly is reduced to synonymy with Philophthalmidae which has priority.

Identification of the present species is complicated by the fact that at least 21 species of *Philophthalmus* have been named, including the following which were not listed by Alicata and Ching (1960): *P. posaviniensis* and *P. cupensis* described by Richter, Varzic and Aleraj (1953) and *P. gnedini* Trofimov as listed by Tret'iakova (1948). The differences between some of those species are no greater than the writer observed as variation within the present one. Some of his specimens bear a striking resemblance to *P. nocturnus* but all differ from that species as described by Looss (1907) in having a smaller oral sucker and pharynx, armed cirrus and much less saccate excretory vesicle. Because there is closer agreement with *P. gralli* Mathis and Leger (1910), as redescribed by Sugimoto (1928), the writer's material is identified as that species. A single specimen described by Yamaguti (1934) as *P. nyrocae* differs from *P. gralli* only in the absence of an eye spot in the miracidium. In the present study, an occasional adult worm, although gravid with eggs, contained none in which a miracidium with an eye spot had developed. Because Yamaguti may have been dealing with such a specimen and because such similar trematodes normally produce miracidia that are very much alike, *P. nyrocae* is reduced to synonymy with *P. gralli*. More than likely, other synonymy exists among species of *Philophthalmus* that have been erected on the basis of the size and shape of the testes, and the extent of the vitellaria and cirrus sac which the author found to vary considerably in the present species. For that reason, a critical comparison of megalurous cercariae and correlation with their adults is an important, if not indeed indispensible approach to the problem of speciation in the genus *Philophthalmus*.

REDESCRIPTION OF THE ADULT

Philophthalmus gralli Mathis and Leger, 1910
(Figs. 1-2)

Description (based on numerous specimens obtained from both natural infections in wild birds and experimentally infected chicks; measurements from stained whole mounts).—Elongate, medium-sized distomes with the characters of the genus. Body fusiform with rounded ends in living worms, more lanceolate with hind body expanded in flattened specimens. Cuticle with imbedded spines 0.01 long, confined to ventrolateral regions of fore body, difficult to see except in sections.

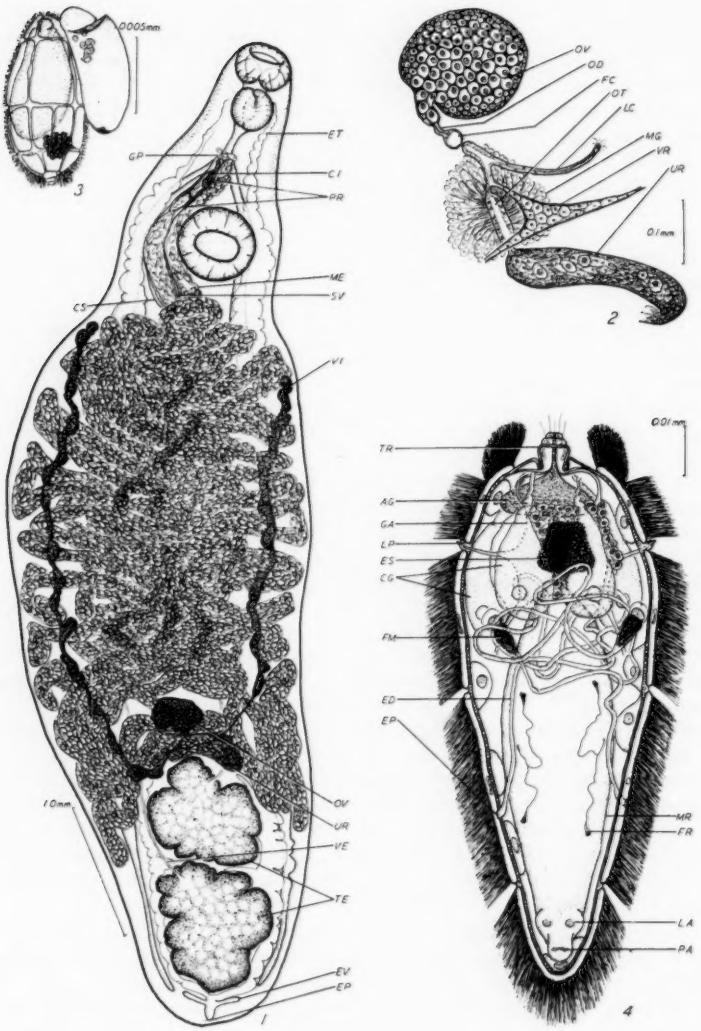
Mature specimens 3.42-8.36 long; 0.67-2.07 in maximum width. Ventral sucker in anterior fourth of body, spherical, 0.43-0.70 in diameter. Oral sucker terminal, 0.20-0.37 long by 0.21-0.47 wide; mouth slightly subterminal, prepharynx very short and wide; pharynx massive, 0.19-0.35 long, 0.17-0.31 wide, wider in sagittal than in frontal plane, its lumen a narrow dorsoventral slit in cross-section. Esophagus usually a little shorter than pharynx, intestinal bifurcation about midway between pharynx and ventral sucker; ceca narrow, reaching posterior end of body, sometimes slightly sinuous or with shallow lateral diverticula.

Testes tandem, entire to distinctly lobed; anterior testis 0.27-1.10 long, 0.25-0.87 wide; posterior testis 0.25-1.01 by 0.21-0.89. Vasa efferentia leave ventral surface of testes near their anterolateral margins and unite before reaching cirrus sac, forming a vas deferens averaging 0.93 long. Cirrus sac dorsal to, or to either side of ventral sucker, slender, 0.83-1.70 long, 0.09-0.32 wide, its extent variable but always overreaching ventral sucker; seminal vesicle sometimes entirely posterior to that sucker. Pars prostatica tubular, averaging 0.19 long; cirrus large when everted, with conical spines 0.005-0.01 long. Genital atrium very shallow if present, the sex openings apparently being separate with female immediately anterior to male.

Ovary submedian, a short distance anterior to testes, circular to oblong in outline, 0.12-0.37 in diameter; with a tail-like extension joining the short, narrow oviduct which enlarges to form fertilization chamber about 0.03 in diameter. Beyond chamber, oviduct is joined first by Laurer's canal which opens to outside dorsally, then by duct of vitelline reservoir. From it vitelline ducts extend laterally ventral to ceca, joining posterior limits of tubular to almost follicular vitellaria ventrolateral to ceca. Anterior extent of vitellaria varying from a level overlapping posterior end of cirrus sac by 0.27 to one not attaining the level of that structure by 0.70; average extent 0.17 posterior to cirrus sac. Mehlis' gland, oötype and proximal portion of uterus posterior to ovary. Uterine coils extensive, occupying width of body from testes almost to ventral sucker, sometimes overlapping anterior testis ventrally and flanking male gonads to midlevel of posterior testis. Metraterm begins posterior to ventral sucker as muscular coils surrounded by unicellular glands, and extends anteriorly parallel to cirrus sac. Eggs numerous; miracidia fully developed, each with double eye spot and containing a redia.

Excretory pore posterior, slightly dorsal; vesicle short, triangular to T-shaped in outline with a very short anterior stem receiving voluminous ascending excretory trunks which extend to sides of pharynx before turning posteriorly as narrower canals; receiving secondary tubes at about level of ventral sucker. Excretory pattern not completely determined but with more flame cells than in cercaria.

Hosts.—Experimental, chicken (*Gallus gallus domesticus*); Natural, green heron (*Butorides virescens*), belted kingfisher (*Megaceryle alcyon alcyon*), bittern (*Botaurus lentiginosus*) and grackle (*Quiscalus quiscula*).



Figs. 1-4.—1. Adult *Philophthalmus gralli* from naturally infected Kingfisher (*Megaceryle alcyon alcyon*), ventral view. 2. Female complex freehand). 3. Miracidium and egg shell, fixed in $AgNO_4$ (freehand). 4. Miracidium enlarged to show details (freehand).

Site.—Orbit at exit of lacrimal duct.

Locality.—Indiana, United States.

Other hosts and localities.—duck (*Anas boschas domestica*), in Formosa; chicken (*Gallus gallus domesticus*), in Indo-China; duck (*Nyroca ferina ferina*), in Japan.

Adult worms in the orbit of experimentally infected chicks cause little noticeable irritation even when the parasites are large or several are present. A tolerance of the parasites may develop gradually as an uninfected bird shows evidence of discomfort for a while when an adult worm from another bird is placed directly in the orbit. The retracted nictitating membrane of infected birds is somewhat more conspicuous than normal and the posterior ends of large worms may project from beneath its free edge.

When removed and placed in 0.85% NaCl or water at room temperature, the worms are very active and frequently protrude the long cirrus. Under these conditions, worms at least 6 weeks of age lay large numbers of eggs which hatch promptly. The distended excretory system is conspicuous and, being transparent, outlines many of the internal organs which can be seen when live worms are projected on a screen. They and the miracidia thus have been used effectively for class room demonstration. The adults also are unusually favorable for research because they are readily removed, subjected to experimental procedures and returned to the orbit of the same or another host. Because the worms do not leave the orbit after reaching it, a single bird may be used for experimental and control parasites, thus eliminating individual host differences as a variable.

DEVELOPMENT IN THE DEFINITIVE HOST

The gonads and cirrus sac of young worms become evident by the 6th day after the chick is fed metacercariae. Sperm in the testes and sometimes the seminal vesicle and female tract appear by the 14th day and, by the 22nd, the uterine seminal receptacle is distended with them. Eggs are present in the proximal uterine coils

---

Abbreviations: AG—apical gland; BP—birth pore; BS—body spines; C_1—cystogenous glands, cell type 1; C_2—same, cell type 2; C_3—same, cell type 3; C_4—same, cell type 4; CG—cephalic glands; Cl—cirrus; CP—ciliated patch; CS—cirrus sac; ED—excretory duct of miracidium; EP—excretory pore; ES—eye spot; ET—excretory trunk of adult; EV—excretory vesicle; FC—fertilization chamber; FM—flame cell of miracidium; FR—flame cell of mother redia; GA—ganglionic mass; GL—glands of metacercaria; GP—genital pore; LA—lateral adhesive appendage; LC—Laurer's canal; LP—lateral papilla of miracidium;—MB—muscle bands of terebratorium; ME—metraterm; MG—Mehlis's gland; MO—mouth of rediae; MR—mother redia; OD—oviduct; OS—oral spines; OT—oötype; OV—ovary; PA—posterior adhesive appendage; PH—pharynx; PO—pores of cephalic gland; PR—pars prostatica; SH—snail heart; SP—sensory papillae; SV—seminal vesicle; TE—testes; TR—terebratorium; UR—uterine seminal receptacle; VE—vas efferens; VI—vitellaria; VR—vitelline reservoir.

by the 14th day and eye spot pigment appears in the developing miracidia about the 31st day but about 35 days are required for the worm to contain eggs that hatch normally and release fully developed miracidia. The adult may persist in the conjunctival sac of the chicken for over 10 months and still contain many eggs in the uterus but it was also observed that the reproductive capacity often was greatly reduced or apparently exhausted in some worms after 75 days.

That the parasite is selective in its growth requirements was demonstrated by subjecting young worms to certain abnormal conditions. Thus, one, taken from the nasal membranes of a hamster infected 19 days earlier, had reproductive organs no further developed than those of a 4-day worm from the orbit of the chick. In the amniotic and yolk sacs of chick embryos, excysted metacercariae developed only about as far in 11 days as they do in the orbit in 3. Finally, 8-day old worms developed no further when removed from the orbit of chicks and maintained in vitro for 30 days.

THE EGG AND MIRACIDIUM

(Figs. 3, 4-7)

The egg is non-operculate and oval with one side slightly flattened. The shell is thin and elastic and has an internal thickening at the small end. When first formed, the shell averages 0.07 by 0.03 and is deep yellow but it attains an average size of 0.11 by 0.05 and becomes pale in color due to stretching as the miracidium develops. When laid by worms placed in 0.85% NaCl, the eggs further enlarge to an average of 0.13 by 0.06 but after hatching, the shell contracts to an average size of 0.09 by 0.04 (Fig. 1). In whole mounts, eggs are noticeably shrunken, fully developed ones in the metraterm averaging 0.08 by 0.04.

When ripe eggs are released from the worm into water or saline, the miracidia become very active and push repeatedly at the large end of the shell until hatching occurs. The lateral papillae apparently do not facilitate that process as Rees (1940) described for the miracidia of *Parorchis acanthus*. Indeed, the cilia beat continuously while the anterior end of the larva is pressed from side to side against the shell until it suddenly ruptures and contracts, forcibly ejecting the miracidium. Although an operculum is not evident, the shell always tears evenly and at the same place so that the large end resembles a cap that remains attached at one point.

Description of the miracidium (measurements from specimens killed in hot 0.2% silver nitrate unless otherwise stated)—oval, 0.10 long by 0.05 wide. Epithelial cells in 4 tiers with nearly always 6, 8, 4 and 2 cells respectively; their nuclei irregularly elongate or stellate. Cells of 1st tier about 0.02 long, triangular with indented base; those of 2nd tier rectangular, averaging 0.03 long; 3rd tier trapezoid, 0.04 long, not always continuing bilateral symmetry of preceeding tiers; 4th tier 0.03 long, capping posterior end of larva. All epithelial

cells with cilia at least 0.01 long in living miracidia; cilia of anterior 3rd of first tier heavier and directed forward. Subepithelium thin, with a few large parenchymal cells scattered beneath a layer of rather evenly spaced circular muscle fibers and fewer scattered longitudinal ones. Two pairs of lateral sensory papillae and 10-12 small circular ciliated patches in space between tiers 1 and 2. Excretory openings posterolateral, between epithelial cells of 3rd tier, usually at about its midlevel. Terebratorium 0.03-0.04 long when protruded, with 4 strong longitudinal muscle bands effecting lateral as well as retracting movements; distal end of terebratorium with 10 papillae, each bearing a sensory bristle. Apical gland filled with large granules, with a syncytial mass containing 4 nuclei at base, and narrow duct opening at tip of terebratorium. Cephalic glands 4, in subdorsal and ventrolateral pairs, difficult to see, dorsal to eye spot and reaching to mid-level of 2nd epithelial cell tier; each gland with 1-3 openings just beneath anterior edge of 1st tier. Large ganglionic mass immediately ventral to the eye spot, with peripheral cells and 6 processes, evidently fiber tracts, 2 extending into terebratorium, 2 to lateral sensory papillae, and 2 posteriorly. Eye spot 0.01-0.02 long, 0.02 wide, each half with indistinct lenticular body. Flame cells 2, large, at mid-level of 2nd epithelial cell tier; their ducts extensively looped at that level, between subdorsal cephalic glands and subepithelium, imbedded in a hyaline mass and expanding to form small terminal ampullae at excretory pores. Contained redia averages 0.08 long by 0.03 wide, occupying most of miracidium posterior to ganglionic mass; excretory pattern of redia 2 [(1)+(1)]; nuclei of pharynx, genital cells and small cement glands leading to 3 posterior appendages visible in living specimens, intestine not evident.

While swimming, the miracidium rotates with the terebratorium telescoped, and is oval in shape with the maximum width at the level of the 2nd tier of epithelial cells (Fig. 4). In water, miracidia swim for 4 to 6 hours during which they become progressively less active. They move toward the source of a beam of light and, upon reaching the edge of the container, may collect there but some immediately swim in the opposite direction. Soon, however, most of them swim about, crossing the beam a few times before again moving with it toward the light source to repeat the swimming pattern. In the presence of the snail, the miracidium may or may not swim at increased speed in a tight circle until it contacts the host and perforates the epidermis with the aid of secretions and the anterior cilia. A crater forms and nearly conceals the penetrating miracidium which, however, does not completely enter the snail's tissues. Instead, the contained redia becomes active and, by pushing the terebratorium to one side, leaves the miracidium within minutes and passes into the lymph spaces of the host. The life cycle therefore differs from that of most digenetic trematodes in lacking a definitive miracidium-sporocyst stage in which germinal multiplication occurs.

FIRST GENERATION REDIA

(Figs. 8, 9, 11)

Small mother rediae were found in the heart of the snail 3 hours after its exposure to miracidia. Although a few such rediae can be found elsewhere in sections, they complete their development only within the heart and do not leave it. That organ becomes enlarged when several rediae are present. The heart of a snail removed 74 days after exposure to miracidia contained rediae of both the 1st and 2nd generations (Fig. 9). They adhere to the endocardium with the 3 posterior adhesive appendages and may be very difficult to dislodge. The tip of each appendage shows many fine indentations (Fig. 11), the openings of glands which secrete a sticky substance.

After 3 months, the redia may be over 1.0 long and has a subspherical pharynx 0.07 in diameter in stained specimens. Numerous papillae with short filamentous projections are irregularly distributed around the mouth (Fig. 8) and a few are scattered over the body. In silver nitrate-treated specimens, the papillae appear as small circles and the intestinal epithelium is delineated as extremely thin polygonal cells with finely irregular borders. The intestine reaches the lateral appendages and is distended with ingested food. Daughter rediae are numerous and escape through a ventral birth pore just posterior to the pharynx.

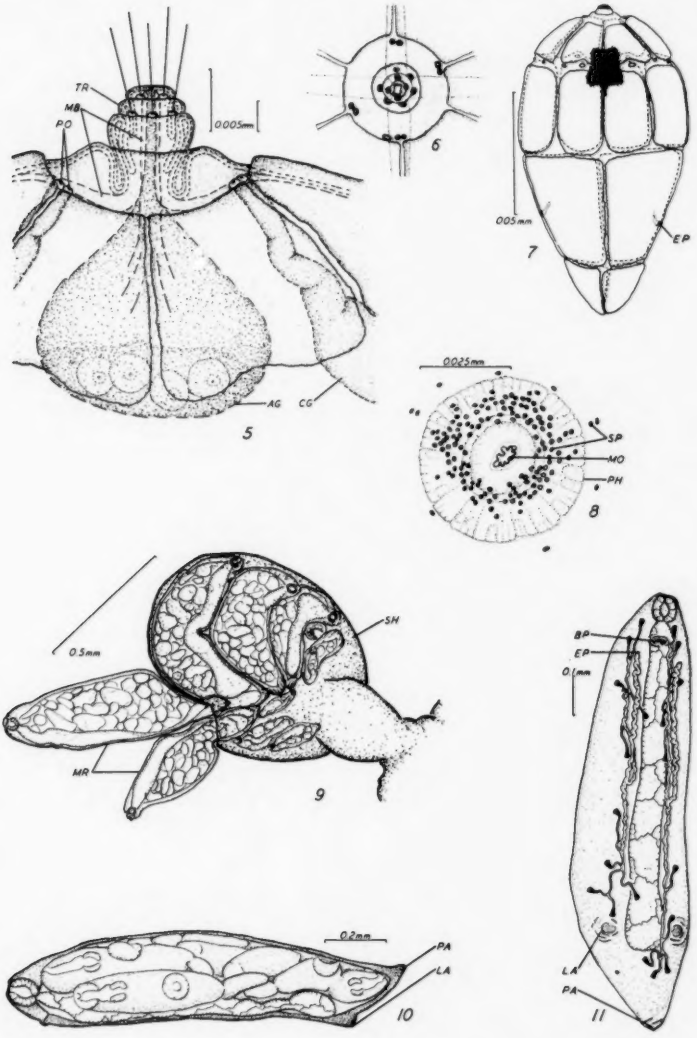
The excretory tubes are tortuous and appear to be imbedded in a hyaline mass loosely adherent to the body wall. Their pores are ventrolateral, just posterior to the birth pore. The flame cell pattern attains a formula of 2 [(5) + (5)] with any group occasionally lacking one flame cell (Fig. 11). The system is asymmetrical in that the last group extends posteriorly farther on the left side than on the right.

SECOND GENERATION REDIA

(Figs. 8, 10, 11)

Six weeks after the snail is infected, daughter rediae can be found free in the circulatory passages of the host, especially those of its kidney and digestive gland. With the dissecting microscope, these rediae, and later the cercariae, may be observed in the intact snail by positioning it so that the mantle and gills are visible with strong substage illumination. The rediae then are seen attached by their posterior appendages to the blood vessels and sway back and forth as the blood flows past them. Small rediae were seen there in old infections but by the time that cercariae emerged, mother rediae could no longer be found in the heart.

The digestive gland is the definitive site at which daughter rediae continue their development and produce cercariae. Morphologically, the two redial generations would be difficult to distinguish were it not for their contained brood. Six months after snails are infected, large daughter rediae killed in hot fixative without pressure average 1.59 long and have a subspherical pharynx 0.05 in diameter.



Figs. 5-11.—5. Terebratorium, showing sensory papillae, muscle bands, glands and their openings (freehand). 6. Same, end view (freehand). 7. Epithelial plates of miracidium (freehand). 8. Sensory papillae of rediae, oral region. 9. Mother rediae in snail heart. 10. Daughter redia. 11. Redia, showing excretory system and gut cells (freehand). (Abbreviations as in Figs. 1-4.)

THE CERCARIA
(Figs. 12-31)

Diagnosis (measurements from spontaneously emerging larvae killed in hot A.F.A. fixative).—With characters of the Megalura Group Sewell, 1922. Body 0.54-0.67 long, 0.12-0.13 in maximum width slightly anterior to ventral sucker, indented at level of that sucker. Tail 0.93-1.14 long, 0.04-0.05 wide at base where its width approximates that of the body; its cuticle unadorned, parenchyma vesicular; posterior one-tenth of tail curved, with terminal invagination receiving ducts of less than 10 unicellular adhesive glands. Oral sucker oval, 0.06 long, 0.04-0.05 wide; ventral sucker 0.06-0.07 in diameter, slightly post-equatorial. Cuticle with many spines 0.01 long, irregularly distributed over entire body except at anterior end. Mouth surrounded by narrow band of spines and by sensory papillae resembling those over body surface and more numerous near anterior end. Prepharynx longer than pharynx; pharynx 0.03-0.04 long, 0.01-0.02 wide; esophagus 0.10-0.11 long but bifurcating well anterior to ventral sucker; ceca reach level of excretory vesicle. Nuclei of genital primordium forms a narrow cord 0.29 long, enlarged at each end. Cephalic glands approximately 20 pairs, mostly lateral to esophagus, with ducts opening anterodorsal to mouth and ventrolaterally in forebody; 2 additional pairs of similar glands in hindbody, with ducts opening just posterolateral to ventral sucker. Body, except at anterior end and around ventral sucker, encased in thick layer of cystogenous material which obscures internal structures. Excretory vesicle small, thin-walled, with subspherical posterior division and smaller anterior chamber receiving separately the primary excretory ducts which extend to prepharyngeal level, expand slightly as they recurve, and terminate just anterior to ventral sucker where each receives anterior and posterior secondary tubules; about 5 ciliated patches in recurrent arm of each primary duct; flame cell formula 2 [(3+3+3)+(2+2+2)]. Develops in 2nd generation redia with long intestine; encysts on various surfaces, preferring exoskeleton of arthropods.

Hosts.—*Goniobasis* spp., *Pleurocera acuta.*

Locality.—Indiana, U.S.A.

Goniobasis sp. in southern Indiana shows a consistently higher incidence of infection with the cercaria of *P. gralli* than does *Pleurocera acuta* from the Tippecanoe River but yields far fewer cercariae per snail. It was observed that emergence from both hosts was stimulated when they were placed in the dark after being exposed to light and that when desired, large numbers of cercariae could be obtained by placing snails in the dark after prolonged exposure to light. Then, larvae usually began to emerge within a few minutes and the process was largely completed within 2 hours. When infected snails were placed in the dark for a time and then positioned under the dissecting microscope so that the mantle and gills could be observed through the aperture of the shell, numerous cercariae were

seen in the blood vessels but disappeared from them after exposure to light for a few hours. It was further observed that when mature daughter rediae were removed from the snail and placed in 0.45% NaCl, those kept in the dark released from 5 to 20 times as many larvae as did those in the light. It thus seems that the stimulus of darkness acts directly on the parasites.

The cercaria of *P. gralli,* like that of *Parorchis acanthus,* is a poor swimmer. In both species, the body flexes strongly and then straightens suddenly in such a manner that the body and tail seem to undulate together. The tail of *P. gralli,* however, is less muscular and has more the appearance of a trailing structure, the tip of which often attaches to objects. Although swimming movements then resemble efforts to pull away, the larva seems able to control attachment by means of the invaginated tail with its associated glands.

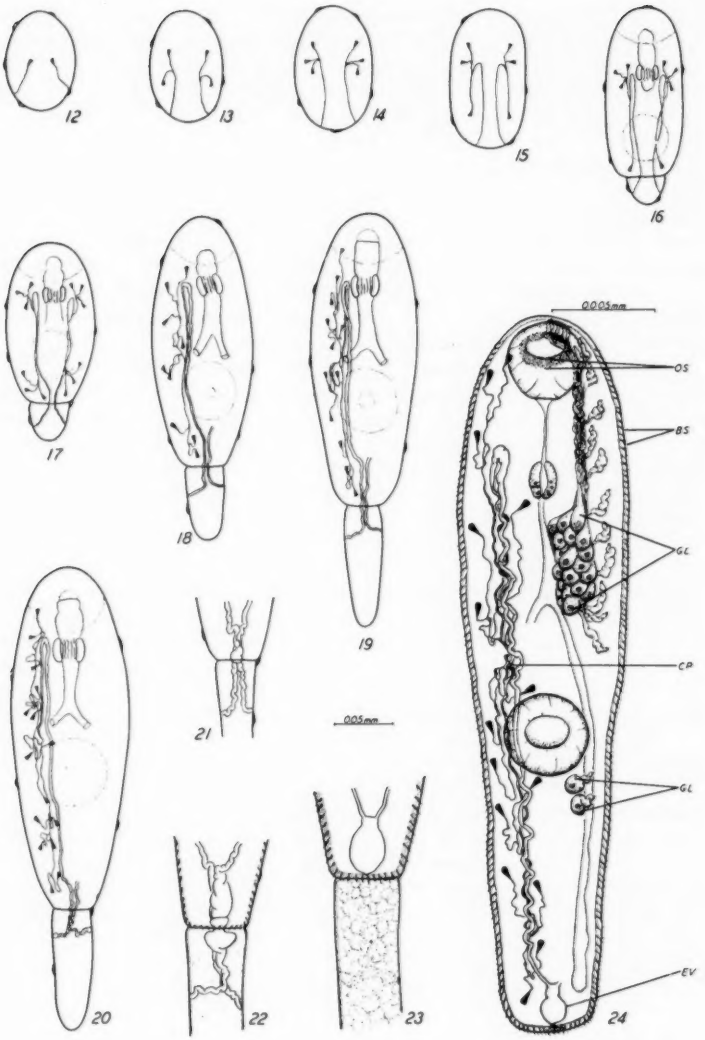
If undisturbed, the cercaria may encyst on the bottom of the dish but that process is hastened and more of the larvae form typical cysts if there is movement of the water. Normally, however, contact is made with crayfish, often between its antenna or a process of the exoskeleton and the tail of the cercaria which immediately bends around that structure. The larva then fastens with its ventral sucker and promptly encysts.

The cercaria of *Philophthalmus gralli* possibly is *Cercaria megalura,* a species which, as Cort (1915) pointed out, was erroneously included in the life history of *Megalodiscus temperatus* by Cary (1909). However, the present larva differs in several respects from *C. megatura* as described by Cort. He observed glands (bâtonnet cells) with cytoplasmic rodlets instead of granular cystogenous material that encases emerging cercariae, and he did not observe cuticular spines. Although other differences may be attributed to incompleteness of his observations and preparation of material, the situation with respect to the cystogenous glands and their function needs to be explored further. I searched especially for bâtonnet glands in spontaneously emerging cercariae and embryos of all ages but such glands were not found. Instead, a complex of other glandular structures was observed in some detail and will be described in connection with encystment. On the basis of cystogenous glands alone, the larvae of *P. gralli* and *C. megalura* would seem to be distinct species and the writer is inclined to regard them as such for the time being.

EMBRYOLOGY OF THE CERCARIAL EXCRETORY SYSTEM

(Figs. 12-23)

Development of the excretory system in the cercaria is first evident in embryos that have begun to elongate and show on each side a flame cell with a ciliated capillary duct opening posterolaterally (Fig. 12). A 2nd and then a 3rd flame cell appear on each side and the primary pores become more posterior (Figs. 13-14). When the beginning of the tail is barely evident, the primary ducts are recurved



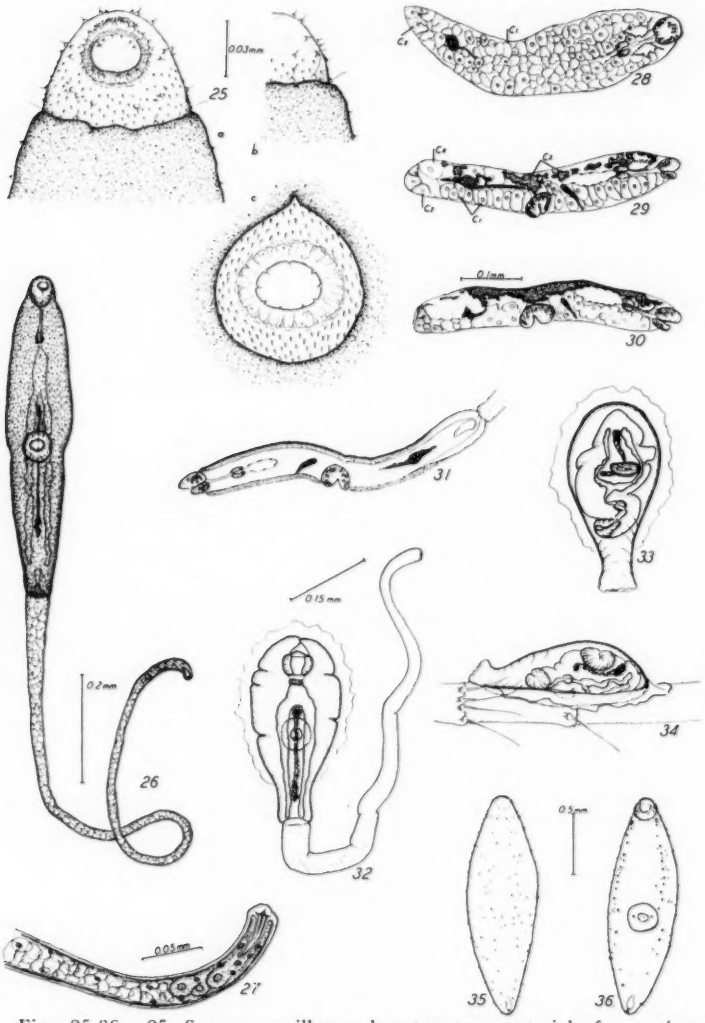
Figs. 12-24.—12-20. Developmental stages of cercarial flame cell pattern (freehand). 21. Excretory vesicle forming (freehand). 22. Same, later. 23. Same, completed, caudal excretory ducts degenerating. 24. Metacercaria showing spines, glands and excretory system (freehand). (Abbreviations as in Figs. 1-4.)

and receive a short anterior capillary with 2 flame cells and a much larger posterior one with a single flame cell (Fig. 15). By the time that the tail bud is well formed and primordia of the suckers, pharynx and esophagus are evident, the 2 anterior flame cells on each side are joined by a third (Fig. 16). Then 2 more flame cells appear near the posterior one on each side (Fig. 17) and the capillaries of three additional ones join each anterior secondary tubule (Fig. 18). The primary pores become relatively farther anterior at the sides of the tail bud and the primary tubules come close together posterior to the ventral sucker. With further growth of the embryo, 3 more flame cells are added to the 6 joining each anterior secondary tubule (Fig. 19) and then 3 to those joining the posterior tubule (Fig. 20). The excretory pattern of the emerging cercaria thus is completed before the posterior ends of the primary tubules fuse to become the excretory vesicle. Excretory structures in the tail then atrophy (Fig. 23) and are not evident in the emerging cercaria.

CYSTOGENOUS GLANDS

Evidently, glands of at least 4 types secrete cystogenous material that was observed at the surface of the fully developed cercaria. In the embryo (Figs. 28-29), 1 type (C_1) occupies the ventral region of the body and consists of large cells with cytoplasm containing numerous eosinophilic granules which are spherical and 1 - 2 μ in diameter. These glands may correspond to those described by Cort (1915) as containing rod-shaped granules in *C. megalura*. A 2nd type (C_2) consists of a smaller number of distinct cells at the posterior end of the body; they contain minute granules that stain more intensely with eosin. The 3rd type (C_3) is in the dorsal half of the body; they extend almost its entire length and produce granular masses that stain dark with hematoxylin; they have obscure cell boundaries. In the hind body, those masses are interrupted by the 4th type (C_4) which are large and contain globules that do not stain with either hematoxylin or eosin. In the older embryo (Fig. 30), boundaries of cystogenous glands become less distinct and their products condense beneath the cuticle as a dark blue dorsal layer and an eosinophilic ventral one.

Secretions of the 4 types of glands combine in a definite pattern to form the material encasing the emerging cercaria (Fig. 31). The secretions of the C_4 cells cover the posterior end of the body to a thickness of about 10 μ dorsally, somewhat less ventrally, and diminish anteriorly, apparently disappearing at the level of the genital primordium. That material is slightly pink and is intermixed with minute granules from the C_2 glands. The remainder of the cystogenous material surrounding the larva is made up of a layer of large eosinophilic granules from the C_1 glands and, on the dorsal surface only of most of the body, an outer basophilic layer from the C_3 glands. The eosinophilic layer is thicker ventrally and thins out



Figs. 25-36.—25. Sensory papillae and cystogenous material of cercaria; a and b, anterior end; c, ventral sucker (freehand). 26. Cercaria. 27. Tip of cercarial tail (freehand). 28. Embryo cercaria, frontal section showing ventral cystogenous glands. 29. Same, sagittal section showing cystogenous glands. 30. Same, later. 31. Cercaria, showing distribution of cystogenous material on surface of body. 32. Cercaria encysting. 33. Metacercaria cyst. 34. Same, on crayfish antenna. 35-36. Metacercaria, $AgNO_3$ fixed, showing sensory papillae; dorsal and ventral views respectively. (Abbreviations as in Figs. 1-4.)

posteriorly as the secretion from the C_4 glands increases in thickness, the 2 together maintaining a uniformly thick layer. The basophilic layer becomes very thin posteriorly but extends farther around the body to encompass the posterior end.

ENCYSTMENT AND THE METACERCARIA
(Figs. 24, 32-36)

Before encystment of the cercaria, the acetabulum attaches firmly to a surface which the forebody explores at various angles. Suddenly, the forebody retracts against that surface and a minute amount of a thick substance is exuded through the layer of cystogenous material. Apparently, that exudate and fine wrinkling movements of the body wall cause the dorsal layer of basophilic material to separate from the eosinophilic layer. The basophilic substance then forms the attached part of the cyst and its exposed surface against which the inner layer is molded. Meanwhile, both suckers are strongly retracted into the body of the larva (Fig. 32). Next, its strong contractions evidently force out additional fluids as the eosinophilic layer of granules rapidly soften and the anterior two-thirds of the body tamps that material against the outer cyst wall. Meanwhile, the posterior region of the body remains stationary with the tail still attached, thus determining the peculiar flask shape of the cyst and preventing the deposition of inner cyst material at its narrow end where, as a result, the cyst is thin and fragile. During the first 3 minutes, the inner cyst layer is largely completed and the posterior end of the body becomes active. It then retracts from the neck of the cyst to which the tail may or may not remain attached, and as movements of the larva continue, the suckers evert and the non-staining material over the posterior body region dissolves and swells to fill the neck end of the cyst with a clear semi-solid mass. Although the worm bends and applies the oral sucker repeatedly to the posterior region, release of material from the cephalic glands was not observed. Finally after 10-15 minutes, the larva becomes oriented with the anterior end toward the narrow end of the cyst and thereafter is relatively inactive (Figs. 33-34).

The metacercaria is infective immediately after encystment and undergoes no apparent development during the two weeks or longer that it may remain alive within the cyst. Quick movements are stimulated by a rise in temperature. If that change is sudden, the worm immediately extends its full length in a single movement with the result that the fore body emerges through the neck of the cyst, followed more slowly by the hind body. If the change is more gradual as probably occurs under normal circumstances, the larva emerges less abruptly but begins immediately to migrate away. Numbers of excysted metacercariae thus can be obtained for experimental purposes by pouring warm saline or water over the cysts as reported by Alicata and Ching (1960).

MIGRATION AND LOCALIZATION IN THE DEFINITIVE HOST

Excystment of the metacercariae occurs immediately upon reaching the mouth or crop of the bird and not in the stomach or intestine as in many other digenetic trematodes. Within 3 to 5 hours after ingestion, immature worms may be found not only in the esophagus but also the nasal passages, the orbit and the lobes of the lacrimal gland. Worms were found on the nasal membranes as long as 4 days after infection but thereafter only in the orbit.

The presence of young worms in the nasal passages on the 4th day suggested that they may migrate back and forth from the eye to the nose at will. However, when such worms were transferred from donor chicks directly to the orbit of others, subsequent examination of their nasal membranes never revealed the parasite, thus indicating that once it reaches the orbit, it remains there. The relationships of the nasal passages, nasolacrimal ducts, and their openings suggest that trematodes found on the nasal membranes of chicks had strayed from the direct route to the orbit after leaving the pharynx of the host.

Because nearly all digenetic trematodes, including some philophthalmids, are endoparasites which localize deep within the bodies of vertebrates, the question is raised as to factors responsible for the unusual habitat of *Philophthalmus* species and for their reaching that site. Among those factors that may be mentioned are geotropism, acidity of the proventriculus as a barrier to migration, chemotactic response to nasolacrimal secretions, temperature effects and the high oxygen tension of the orbit.

Although there is an abundance of free oxygen in the orbit, it is difficult to conceive how a gradient could effect migration of worms to that site. Furthermore, when even large numbers of worms were placed in Warburg respirometers and were permitted to remain there for several hours, there was no evidence of oxygen consumption (personal communication, Fisher).

Since metacercariae normally excyst before exposure to the acid secretions of the proventriculus, it was thought that those fluids might repel worms migrating downward, causing them to move in the opposite direction. To test that possibility, use was made of T-tubes filled with 10% fresh egg albumin in 90% Tyrode's balanced salt solution with phenol red as an indicator and made slightly alkaline with sodium carbonate. Proventricular secretions were introduced at one end of the straight side and a narrow beam of light directed through its intersection with the stem in such a manner that convection currents produced a relatively sharp acid-base interface at that point. Excysted metacercariae were then introduced through the stem and their actions followed. It was observed that: (1) Only rapidly migrating worms entered the acid region and then only a distance of about one-eighth inch before stopping and searched about with the forebody. Those unable to find their way out eventually

died. (2) Those moving slowly stopped immediately upon reaching the interface, performed searching motions with the forebody and then withdrew from the interface, moving parallel or at an angle to it. (3) After 1-2 hours, those worms remaining in the alkaline region of the tube continued to move about while those in the acid medium were either apparently dead or lying at the bottom of the tube where they showed weak movements. Although this experiment indicated that the acidity of the proventriculus repels young worms and thus starts them to move up the esophagus, it did not account for their continued migration in that direction to the pharynx and their choice of the orbit by way of the nasolacrimal duct over other sites available through natural passage from the pharynx.

The rapidity with which the young worms can reach the lacrimal glands suggested that its secretions may elicit a chemotactic response on the part of the parasite. To test that possibility, attempts were made to tie off the nasolacrimal duct and thereby block the flow of such secretions, but due to the large size and very thin walls of the duct, the operation was successful in only one bird. Both encysted and free metacercariae were introduced into its proventriculus and crop. Three hours later the worms were found in the esophagus and crop only. The tear secretions were diverted to the outside in another bird in which healing of surgically traumatized ducts blocked them. When it was fed metacercariae and examined several weeks later, no worms were found anywhere. Substitution of excised tear glands for proventricular secretions in the T-tube apparatus showed only that the gland tissue when not intact, apparently is toxic to the parasites.

Although chemotactic response of the parasite to nasolacrimal secretions was not demonstrated in vitro, such a role is compatible with failure of Alicata and Ching (1960) and the writer to infect mammals by the oral route. As Bang and Bang (1959) pointed out, the lacrimal ducts of most mammals drain into the anterior portions of the nasal passages and secretions mostly flush the vestibule and spill out the nostrils. Thus they would not all be swallowed as probably occurs in the bird to serve a possible chemotactic role. Also, in such mammals, worms migrating to the eye by way of the nasolacrimal duct would be subject to greater temperature fluctuation than in birds in which the duct opens much farther from the nostrils. When young worms were placed in a petri dish of saline and a small central area warmed, they moved into that area and once there did not leave it. Instead, they concentrated in a small circle near its edge and reacted to the adjacent cool area much as they did to the acid-base interface as described above.

Alicata and Ching (1960) postulated that the occasional human infections may have been acquired by direct ocular infection which they found successful with mammals that could not be infected by the oral route. However, the nasolacrimal ducts in man drain into

the posterior nasal passages as they do in birds, and man may be more susceptible to infection by the oral route than those mammals that have proved to be refractory.

REFERENCES

ALICATA, J. E. AND H. L. CHING 1960. On the infection of birds and mammals with the cercaria and metacercaria of the eyefluke, *Philophthalmus*. *J. Parasitol.*, **46**:16.

BANG, B. G. AND F. B. BANG 1959. A comparative study of the vertebrate nasal chamber in relation to upper respiratory infections. *Bull. Johns Hopkins Hospital*, **104**:107-149.

CABLE, R. M., R. S. CONNOR AND J. W. BALLING 1960. Digenetic trematodes of Puerto Rican shore birds. *New York Acad. Sci.*, **17**:185-255.

CARY, L. R. 1909. The life history of *Diplodiscus temperatus* Stafford. With especial reference to the development of the parthogenetic eggs. *Zoologische Jahrbucher. Abt. für Anat. und Ontog. der Tiere*, Jena, **28**:595-659.

CHING, H. L. 1960. Some digenetic trematodes of shore birds at Friday Harbor, Washington. *Helminthol. Soc. Wash.*, **27**:53-62.

CORT, W. W. 1915. Some North American Larval trematodes. *Illinois Biol. Monogr.*, **1**:447-532.

DAWES, B. 1956. *The Trematoda With Special Reference to British and other European Forms*. 2nd edition, Cambridge at the University Press, London. 644 p.

DUBOIS, G. AND J. MAHON 1959. Etude de quelques trematodes Nord-Americains suivie d'une revision des genres *Galactosomum* Looss 1899 et *Ochetosoma* Braun 1901. *Bull. Soc. neuchateloise Sci. nat.*, **82**: 191-229.

FISHER, F. M. AND A. F. WEST 1958. *Cercaria megalura* Cort, 1914, the larva of a species of *Philophthalmus*. *J. Parasitol.*, **44**:648.

LAL, M. B. 1936. A new species of the genus *Parorchis* from *Totanus hypoleucos*, with certain remarks on the family Echinostomidae. *Proc. Indiana Acad. Sci.*, **4**:27-35.

LA RUE, G. R. 1957. The classification of digenetic Trematoda: a review and a new system. *Exp. Parasitol.*, **6**:306-349.

LOOSS, A. 1899. Weitere Beiträge zur Kenntniss der Trematoden-Fauna Aegyptiens, zugleich Versuch einer natürlichen Gliederung des Genus *Distomum* Retzius. *Zoologische Jahrbücher. Abt. für Syst., Oekol. und Geog. der Tiere*, Jena, **12**:521-784.

———1907. Notzen zur Helminthologie Aegyptiens. VII. Uber einige neue Trematoden der ägyptischen Fauna. Zentralblatt für Bacteriologie, Parasitenkunde und Infectionskrankheiten. Erste Abteilung. *Originale.*, **43**:478-490.

LYNCH, J. E. 1933. The miracidium of *Heronimus chelydrae* MacCallum. *Quar. J. of Microscop. Sci.*, **76**:13-33.

MATHIS, C. AND M. LEGER 1910. Douve oculaire de la poule. *Bull. Soc. de Pathol. Exotique*, **3**:245-251.

POCHE, F. 1926. Das System der Platodaria. *Arch. für Naturgeschichte*. Abteilung A, **91**:1-240.

REES, G. 1940. Studies on the germ cell cycle of the digenetic trematode *Parorchis acanthus* Nicoll. Part ii. Structure of the miracidium and germinal development of larval stages. *Parasitology*, **32**:372-391.

RICHTER, S., O. VARZIC AND Z. ALERAJ 1953. Filoftalmoza domaće guske. *Veterinarski Arch.*, **23**:193-205.

SEWELL, R. B. S. 1922. Cercariae indicae. *Indian J. Med. Res.*, **10**:1-370.

STUNKARD, H. W. AND R. M. CABLE 1932. The life history of *Parorchis avitus* (Linton), a trematode from the cloaca of the gull. *Biol. Bull.* **62**: 328-338.

SUGIMOTO, M. 1928. On the trematode parasites (genus *Philophthalmus*) found in the eyes of Formosan domestic birds. (in Japanese). *J. Japanese Soc. Vet. Sci.*, **7**:22-34.

TRAVASSOS, L. P. 1918. Novo typo de Philophthalmidae. *Rev. Soc. Brasileira Sci.*, **2**:75-77.

TRET'IAKOVA, O. N. 1948. Two new helminths of birds of the Cheliabinsk oblast — *Philophthalmus muraschkinzwei* and *Tatria skrjabini* n. sp. (in Russian). Sbornik Rabot po Gel-mintologii. (K. Sorokaletiia Nauchnoi Deiatel'nosti Akademika K. I. Skriabina), p. 232-236.

YAMAGUTI, S. 1934. Studies on the helminth fauna of Japan. Part 3. Avian trematodes, ii. *Japanese J. Zool.*, **5**:543-583.

———1958. *Systema Helminthum.* 1st Ed. Interscience Publishers, Inc., New York, 1575 p.

Life History of the Pigmy Salamander, Desmognathus wrighti, in Virginia

JAMES A. ORGAN

Department of Zoology, University of Michigan, Ann Arbor

ABSTRACT: Eggs of *Desmognathus wrighti* containing late embryos were found on October 16, 1958, at Whitetop Mountain, Smyth County, Virginia. Transformation in this species occurs prior to hatching. The eggs, hatchlings, and hatching process are described and figured. Recently captured adults of this species engaged in courtship during the fall and spring of 1958-59. The courtship pattern, sex recognition method, and aggressive behavior are described and the spermatophore is described and figured.

INTRODUCTION

During a field study of the ecology of the plethodontid salamanders in the Mount Rogers-Whitetop Mountain area of Virginia, data were obtained concerning several aspects of the life history of *Desmognathus wrighti*. The eggs, hatchlings, and spermatophores were observed in the field and/or the laboratory and are described and figured herein for the first time. The hatching process, courtship, and aggressive behavior were also studied. Specimens discussed in this paper are in the collection of the Museum of Zoology of The University of Michigan.

Travel expenses in the field during the summer of 1958 were defrayed, in part, by a grant from the Horace Rackham School of Graduate Studies of The University of Michigan and funds from an anonymous donor made possible the continuation of the studies during the month of October, 1958. I am indebted to Nelson G. Hairston, Charles F. Walker, and Frederick R. Gehlbach for reading and criticizing the manuscript and to my wife, Della S. Organ, for her assistance in the field and laboratory.

NESTING SITE

Six clusters of *D. wrighti* eggs were discovered on October 16, 1958. All of the clusters were beneath the bank of the headwaters of Big Branch Creek on the north side of Whitetop Mountain, Smyth County, Virginia, at an altitude of 4350 feet. The eggs were at a depth of about 12 inches in a pocket of gravel and mud through which water percolated. The site was saturated and several larvae of *Pseudotriton porphyriticus* and *Eurycea bislineata wilderae* were taken near the egg masses. Excavation of the site was difficult because the bottom of the hole filled with water and the walls collapsed. The final excavation measured three feet on a side by one foot deep.

Each cluster of *D. wrighti* eggs were suspended from the side or the bottom of a small rock with the bulk of the mass projecting into a

small cavity in the mud surrounding the rock. There was only one cluster in each of the small cavities but some of the clusters were within a few inches of one another.

Five egg clusters of *Desmognathus ochrophaeus carolinensis* were also found in this site in "nest cavities" quite similar to those of *D. wrighti.* In addition to the eggs and larvae, 123 *D. wrighti,* 39 *D. o. carolinensis,* 9 *D. f. fuscus,* 4 *E. b. wilderae,* and 3 *P. porphyriticus* adults were collected in the excavation. After removing the eggs, larvae, and adults, the excavation was carefully filled in.

The site was re-examined the following spring. On April 16, 1959, 352 *D. wrighti* were removed from the site. On May 16, 1959, an additional 147 *D. wrighti* were taken in the excavation, but on June 13, 1959, only 26 *D. wrighti* were found. The first snow of the 1958-59 winter season fell on Whitetop Mountain October 25, 1958, shortly after the site was discovered. In early April, 1959, snow was still on the ground in this area. It can be concluded, therefore, that the 649 specimens of *D. wrighti* removed from the nest site in the fall and spring represented a hibernating aggregation.

EGG MASS AND ATTENDING FEMALE

The clusters of *D. wrighti* eggs found on October 16 contained pigmented embryos in late stages of development. The exact number and placement of the individual egg capsules could not be determined, but there were at least two and possibly three concentric transparent capsules. Prior to preservation, the outer capsule of each egg had a diameter of 3.5 mm.

Each mass was a compact cluster of from 3 to 8 eggs (Fig. 1A) suspended by a single attachment stalk. The attachment stalk was merely an extension of the outer capsules of one or two of the central eggs of the mass. Outer capsules of the peripheral eggs of the mass adhered to those of the more central eggs.

An adult was seen with each egg mass but mud-slides, collapsing the walls of the excavation, prevented recovery of the attending adults with their eggs in all but two instances. The two attending adults, taken with their eggs, were females with recently spent ovaries and enlarged convoluted oviducts.

Prior to preservation, the attending females were kept with their eggs in captivity. Each female remained close to her egg mass with the body coiled around the mass and the head either resting upon the eggs or thrust into the center of the mass. Neither female attempted to defend the eggs when disturbed by the observer; both females retreated from the eggs but returned to them shortly after the disturbance ended.

HATCHING PROCESS

Since field work was suspended on October 26, it was not possible to bring all of the egg clusters through to hatching. Four of them,

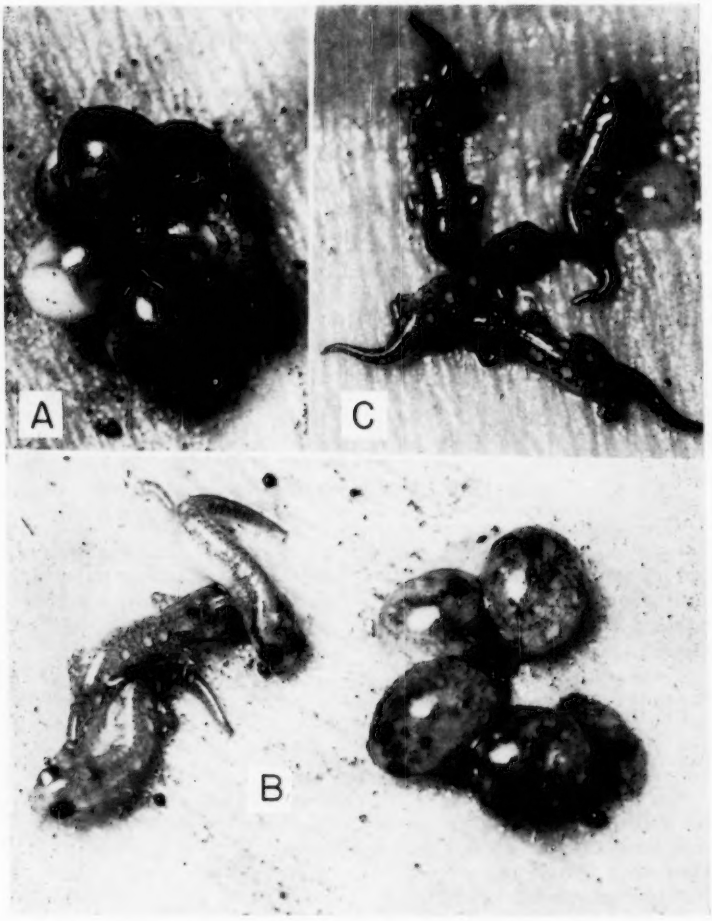


Fig. 1.—Hatching sequence of *Desmognathus wrighti*. A. Eggs containing late embryos; photographed October 16. B. Eggs in process of hatching and hatchlings; photographed October 22. C. Recently hatched young approximately 12 hours after hatching; photographed October 23.

however, hatched either partially or completely in the laboratory (Table I). As the eggs approached a hatching condition, they changed in shape from spheroids (Fig. 1A) to ovoids (Fig. 1B). The encapsulated embryos engaged in vigorous pre-hatching movements, thrusting the head and appendages against the inner capsule (or capsules). They also rotated within the eggs propelling themselves with

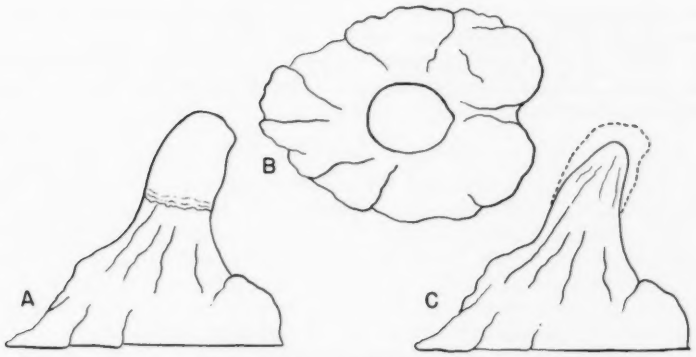


Fig. 2.—Spermatophore of *Desmognathus wrighti*. A. Right lateral view. B. Dorsal view. C. Right lateral view of stalk with position of sperm cap indicated by dotted line.

the aid of the limbs, tail, and flexing of the body. The capsules appeared to weaken in the region of the snout and then rupture. The head and forelimbs of the hatchling were expelled through the rupture points with the escaping egg fluid. The hind limbs and tail were usually freed from the collapsed egg capsules immediately but a few of the young remained in a "semihatched" position for a short period of time. At hatching the young were well coordinated and capable of walking. During the first 24 hours following hatching, they usually

TABLE I.—Clutch number, hatching dates and hatchling size in *Desmognathus wrightii*

Clutch number	Number of eggs	Date hatched	Number hatched	Mean length at hatching in mm	
				Snout-vent	Total
1	3	.....	..	....	.....
2	8	.....	..	....	.....
3	6	Oct. 19-20	6	7.4	10.0
4	5	Oct. 21	2	7.0	10.3
5	7	Oct. 22-23	7	7.9	11.3
6	8	Oct. 24-25	7	8.1	11.2

remained close to the egg capsules but some immediately left the vicinity of the eggs and climbed the glass walls of the finger bowls in which the eggs were kept.

In general embryos within the capsules and recently hatched young were negatively phototropic. The encapsulated embryos rotated until the head was directed away from the light source with the bulk of the body and yolk situated between the eyes and the light. The

hatchlings moved under cover or, in the absence of cover, moved to the less brightly lighted areas of the container.

Many of the hatchlings shed the skin at least once during the first 24 hours after hatching. This same behavior was observed in hatchlings of *Plethodon welleri.*

RECENTLY HATCHED YOUNG

In contrast to other species of *Desmognathus* with known life histories, the hatchlings of *D. wrighti* are not larvae. Gills, present in late embryonic stages as three pairs of long, slender, unbranched, pigmentless structures, are resorbed prior to hatching. The tail of the late embryo is slightly compressed but that of the hatchling is circular in cross section. Caudal fins are lacking in both the late embryos and hatchlings. Mean snout-vent and total lengths of the broods for each clutch are given in Table I.

At hatching the ventral surfaces of the chin, belly, and tail, as well as the undersurfaces of the limbs, are unpigmented. The margin of the lower jaw is pigmented by scattered melanophores. The dorsal pigmentation is determined by the presence or absence of melanophores; no other pigment cells are evident. The unpigmented stripe between the posterior border of the eye and the angle of the jaw, characteristic of this genus, is present in the late embryo and the hatchling. The snout is either unpigmented or lightly pigmented, a condition present in recently transformed individuals of *D. ochrophaeus* (Bishop, 1941).

Well-defined paravertebral spots are present and extend from above the axilla to the proximal two-thirds of the tail (Figs. 1B and 1C). These spots appear yellow in life but are unpigmented. The yellow color results from the underlying yolk mass. The margins of the spots are heavily outlined by concentrations of melanophores. There is another concentration of melanophores in the mid-dorsal line of the trunk, probably representing the anlage of the herring-bone pattern characteristic of the adults of this species. The mid-dorsal line of the distal half of the tail bears an unpigmented stripe.

Three of the five clusters of *D. o. carolinensis* eggs, collected at the same time and in the same site as those of *D. wrighti,* hatched in captivity between October 20 and October 25. Eggs of both species were maintained in the laboratory under the same conditions. Since all of the hatchlings of *D. o. carolinensis* emerged from the eggs as larvae with well-developed gills and caudal fins, it is unlikely that conditions of captivity induced abnormal prehatching transformation in *D. wrighti.* It can be concluded that transformation in *D. wrighti* normally occurs within the egg.

COURTSHIP

Recently captured adults of *D. wrighti* were maintained in 8-inch glass finger bowls throughout the summers of 1957 and 1958, the fall of 1958, and the spring of 1959. Captives were kept on a sub-

strate of moist paper toweling and replaced by fresh salamanders at intervals of two weeks. Spermatophores were found in the containers on the mornings of October 8, April 18, April 20, April 30, May 21, and May 22. Courtship behavior was witnessed during the nights of September 6-7, April 19-20, and May 20-21. Thus, *D. wrighti* has both a fall and a spring courtship period.

The courtship patterns of this and three other species of *Desmognathus* have been described in detail elsewhere (Organ, in press). Sex recognition is accomplished by means of behavioral responses on the part of the individual approached by a courting male. Females either flee from a courting male or remain passive. Males either flee, remain passive, or attack a courting male by biting him. The most frequent response by a male to a courting male is an attack.

The preliminary courtship phases are characterized by the male placing his snout on the dorsum of the female and arching his body upward with the belly and forelimbs raised clear of the ground. The snout and hindlimbs of the male act as anchor points for the arching body. The male violently straightens his body from the arched position and then repeats the arched posture with his snout pressing down on the dorsum of the female. Preliminary stages of courtship are followed by a typical plethodontid tail-straddling walk during which a spermatophore is desposited on the ground by the male (Noble & Brady, 1930; Stebbins, 1949; Organ, 1958, 1960a, 1960b). The tail-straddling walk is usually terminated when the female picks up a sperm cap from a spermatophore with her cloacal lips. The stalk of the spermatophore remains adherent to the ground.

SPERMATOPHORE

In gross appearance the spermatophore of *D. wrighti* (Fig. 2) resembles that of *D. fuscus,* as figured by Bishop (1941), but is smaller. It is 2.5 mm high. There is a colorless, glass-like, jelly stalk and a milky white sperm cap. The stalk is slender and conical with a flaring base of attachment to the substrate. Viewed from above, the base of the stalk is heart-shaped (Fig. 2B). The sperm cap is merely a thin sheath covering the tip of the spike-like stalk. When removed from the stalk, the sperm cap collapses into an amorphous mass.

The surface of the sperm cap is adhesive and clings to objects placed in contact with it. It does not cling to the belly of a courting female, however, when she passes over it. The sperm cap is the only portion of the spermatophore recovered by the female. When recently picked up, it is held between the cloacal lips at the anterior angle of the vent. Eventually, it is withdrawn into the cloaca and ultimately reaches the vicinity of the spermatheca.

The collapsing of the sperm cap into an amorphous mass is typical of the spermatophores of *Desmognathus* in contrast to those of *Plethodon* (Organ 1958, 1960a, 1960b). In the latter genus, the cap retains its shape after being detached from the stalk and does not collapse.

REFERENCES

BISHOP, S. C. 1941. The salamanders of New York. *New York State Mus. Bull.*, **324**: 1-365.

NOBLE, G. K. AND M. K. BRADY 1930. The courtship of the plethodontid salamanders. *Copeia*, **1930**(2): 52-4.

ORGAN, J. A. 1958. Courtship and spermatophore of *Plethodon jordani metcalfi*. *Ibid.*, **1958**(4): 251-9.

———1960a. The courtship and spermatophore of the salamander *Plethodon glutinosus*. *Ibid.*, **1960**(1): 34-40.

———1960b. Studies on the life history of the salamander *Plethodon welleri*. *Ibid.*, **1960**(4).

———in press. Studies of the local distribution, life histories, and population dynamics of the salamander genus *Desmognathus* in Virginia. Ecol. Monographs.

STEBBINS, R. C. 1949. Courtship of the plethodontid salamander *Ensatina eschscholtzii*. *Copeia*, **1949**(4): 274-81.

A New Species of Echinostelium from Greece[1]

CONSTANTINE J. ALEXOPOULOS
University of Iowa, Iowa City

ABSTRACT: A new species of *Echinostelium, E. cribrarioides,* developed in moist chamber culture on poplar bark collected in Greece, is described. It differs from the other three known species in that it forms a well-developed, globose capillitial net. A key to the four known species is provided and the description of the order Echinosteliales is broadened to include this species.

Among a number of Myxomycetes which developed in moist chamber culture on bark from living trees collected in Greece by the author in the summer of 1960, one proved to be an undescribed species of *Echinostelium.* Inasmuch as the characters of this species make it necessary to expand our concept of the order Echinosteliales, this brief article appears to be justifiable.

Echinostelium cribrarioides sp. nov.

Sporangia solitaria vel gregaria, 85-120μ diam., 0.3-0.5mm. alta, robusta, erecta vel nutantia, ochroleuca, stipitata; stipes erectus, 0.2-0.35mm. altus; peridium fugax, reliquens collare ad apicem stipitis; columella brevis 4-20μ alta; capillitium ex apice columellae enascens, ramificiens, et reticulum globosum cum paucis terminis liberis formans; sporae globosae, leves cum areolae crassae, pallidae, 9-10μ diam.; protoplasmodium pallidum.

Sporangia stipitate, scattered or gregarious, globose, 85-120μ in diameter, 0.3-0.5mm tall, cream colored; stipe hairlike, varying from almost colorless to dark brown, mostly brown below, lighter toward the top, subulate, expanded below and filled with granular material; columella 4-20μ in height, sharply delimited from the stalk by a conspicuous collar, the remnant of the evanescent peridium; capillitium typically forming a complete, globose net with large meshes, sometimes with one or more free strands extending from it; spore mass cream-colored, supported by the capillitium; spores colorless by transmitted light, 9-10μ (mostly 9.5μ) in diameter, the wall smooth, but conspicuously thickened in several more or less evenly distributed areas; plasmodium a colorless protoplasmodium.

Type (GR-14-1960).—Developed in moist chamber culture on bark collected August 6, 1960, from a living *Populus* sp. growing on Mt. Penteli near the monastery of Daou Penteli, north of Athens, Greece. Deposited in the Macbride-Martin Myxomycete Collection, University of Iowa, Iowa City.

This unusual species is described from abundant material which developed on three pieces of bark from a poplar tree near Athens, collected in August 1960, and brought to Iowa City where it was

[1] Part of National Science Foundation project G-6382: An Experimental Approach to the Taxonomy of the Myxomycetes.

placed in a moist chamber. Two or three hundred sporangia developed about a week after the bark was wet. At first glance it was recognized that these sporangia differed from those of either of the two known species of *Echinostelium,* because of their more robust appearance and considerably larger sporangial heads.

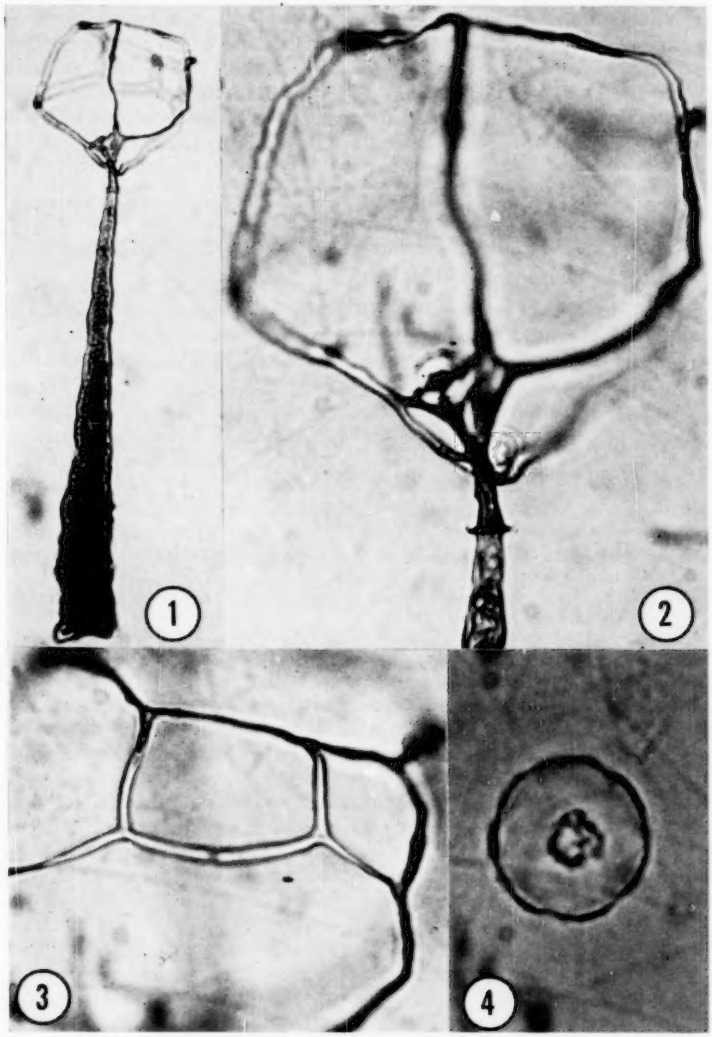
The well-developed capillitial net is the chief characteristic feature of this species (Figs. 1-3). When the sporangia are completely dry, the outer spores of the spore mass are easily dispersed by gently tapping the sporangial stalk with a fine needle. The capillitial net is then exposed often retaining a spore ball inside, giving the fructification the aspect of a *Cribraria,* hence the specific name *cribrarioides* chosen for this species. The peridial collar which remains at the base of the sporangium, and the columella (Fig. 2), from the tip of which the capillitial net originates, leave no doubt as to the nature of the net. It is truly capillitial. The columella and capillitium have a different aspect from that of the stalk. Whereas the stalk is conspicuously granular and in all ways resembles that of *E. minutum* and *E. elachiston* the columella is much less granular, sometimes lacking any granular appearance altogether, and the capillitium is completely homogeneous except possibly at the point of its attachment to the columella.

With transmitted light, the columella and capillitium appear yellow. The capillitial threads are thicker and more robust than those of *E. minutum,* with a diameter of about 2μ

The spores of *E. cribrarioides* are larger than those of two of the other species, but smaller than those of *E. fragilis,* having an average diameter of 9.5μ and a range of 9-10μ. Their structure is characteristic for the genus. The wall possesses a number of thickened areas more or less evenly distributed over its surface. These are particularly conspicuous in the empty spore cases after germination or in spores stained with cotton blue, but can be easily detected in unstained spores under the oil immersion objective (Fig. 4).

Of several attempts to grow this organism in culture only one succeeded. The spores were placed on ½ strength corn meal agar (Difco corn meal agar mixed with equal quantities of 2% plain agar) and a suspension of *Escherichia coli* was poured over them. In about a week several plasmodia had formed. These were colorless protoplasmodia (Alexopoulos, 1960b) much resembling those of *E. minutum* (Alexopoulos, 1960a). The majority of these encysted and could not be induced to develop further. Four, however, proceeded to fruit, each producing a single sporangium. Unfortunately the sporangia in culture were not perfectly developed. The capillitium was rudimentary and obviously aberrant, exhibiting four or five stout main branches but no net. Nevertheless, the nature of the columella and the capillitial branches, the sharp distinction between the stalk and the columella, and the color of the capillitium were all recognizable characters of this species. Attempts to culture the organism again are continuing, but as the material ages the possibility for success becomes smaller.

The discovery of *E. cribrarioides* necessitates a broadening of the description of the order Echinosteliales (Martin 1960) as follows:



Figs. 1-4. *Echinostelium cribrarioides* sp.n.

1. Entire fruiting body after removal of spores × 178.
2. Detail of peridial collar, columella, and origin of capillitium × 530. Detail of upper mesh of capillitial net × 530. Spore × 2400.

Order Echinosteliales

Sporangia globose, stalked, minute. Peridium usually evanescent, rarely persistent. Columella usually present. Capillitium present or absent; when present, either scanty or forming a very open globose net. Spores white, cream-colored, faint pinkish, or golden in mass, colorless, tinged with pink, or golden yellow by transmitted light; spore wall marked with thickened areas, more or less evenly distributed over the surface. Assimilative stage a protoplasmodium.

Family Echinosteliaceae

With the characters of the order.

1. *Echinostelium* deBary; Rost. Versuch. 7. 1873.

With the characters of the family.

Type species, *Echinostelium minutum* deBary.

Capillitium absent

Columella, if present, inconspicuous ..... *E. elachiston*

Columella well-developed ..... *E. fragile*

Capillitium present

Capillitium scanty ..... *E. minutum*

Capillitium a well-developed globose net ..... *E. cribrarioides*

REFERENCES

ALEXOPOULOS, C. J. 1958. Three new species of Myxomycetes from Greece. *Mycologia,* **50**:52-56.

———1960a. Morphology and laboratory cultivation of *Echinostelium minutum* deBary *Am. J. Bot.,* **47**:37-43.

———1960b [1961]. Gross morphology of the plasmodium and its possible significance in the relationships among the Myxomycetes. *Mycologia,* **52**:1-20.

MARTIN, G. W. 1960 [1961]. The systematic position of the Myxomycetes. *Mycologia,* **52**:119-129.

NANNENGA-BREMEKAMP, N. E. 1961. Notes on Myxomycetes IV. Acta Bot. Neerland. **10**:55-66.

A Synopsis of Pinguicula (Lentibulariaceae) in the Southeastern United States

R. K. GODFREY and H. LARRY STRIPLING[1]
Department of Biological Sciences, Florida State University, Tallahassee

ABSTRACT: Six species of *Pinguicula* occurring in the southeastern United States are treated. *P. ionantha* Godfrey is newly described; it is restricted in its distribution to Franklin, Liberty, Gulf and Bay counties, all in the Panhandle of western Florida. A key to the species, descriptions and chromosome counts are included. All species are illustrated.

Wood and Godfrey (1957) in a discussion of the Pinguiculas of the southeastern United States treated five species, four of which had previously been known from the area. *P. primuliflora,* there newly described, had been found to occur from southwestern Georgia and western Florida to southern Mississippi. In addition to the morphological features by which it was distinguished, *P. primuliflora* was noted to occur in habitats unusual for *Pinguicula,* namely, in shady areas of spring runs or springy places with *Sphagnum* or *Pallavicinia,* on grassy tussocks, bases of gum trees, and on mill timbers in association with *Orontium* or *Nymphoides,* almost always where there is flowing water. Some specimens were collected in moist, sandy soils in pinelands but these plants were less well-developed than those from wetter localities. It happens that specimens from the latter, different, type sites comprised two collections from pinelands in Franklin and Liberty counties, Florida, somewhat to the southeast of the more numerous localities for well-developed plants.

During the wet spring of 1960, we visited Franklin and Liberty County localities and discovered well-developed populations of a *Pinguicula* clearly distinguishable from *P. planifolia* and unlike *P. primuliflora* to which species the earlier collections had been assigned. The plants were in shallow standing water of sandy-peaty pineland depressions and broad roadside drainage ditches. Populations of the same plant, again associated with *P. planifolia,* were subsequently located in Gulf and Bay counties, Florida, just to the west. This *Pinguicula* is newly named and described below. The total number of species now known for Florida and the southeastern United States is six.

During the spring seasons of 1960 and 1961 a few plants of each of the six Pinguiculas were collected at several localities, the total being about a hundred plants. They were placed in shallow pans of water in the laboratory where they fourished, producing flowers

[1] This investigation was supported (in part by a research grant, RG-6305, to the senior author from the Division of General Medical Sciences, Public Health Service.

continuously for about six weeks. This provided an opportunity to study the plants at leisure, to have illustrations prepared, to describe them in detail, and to make cytological investigations. A key was prepared which may prove helpful in identifying the species, using living material particularly.

Dr. David M. Moore, University of California, Los Angeles, who is presently investigating *Pinguicula* experimentally, has living material of our species. It is presumed that he will study species from various parts of the world and that his employment of newer techniques and criteria will yield a more definitive understanding of species interrelationships and a reinterpretation of the subgenera as reviewed by Barnhart (1915).

Acknowledgments.—The Latin diagnosis for the proposed new species was provided by Dr. Lloyd H. Shinners, Southern Methodist University, to whom acknowledgment is gratefully made. Illustrations were prepared by Mr. Grady W. Reinert. The generic description below is not meant to be applicable other than to the genus as it occurs in the area under consideration.

GENERIC DESCRIPTION

Plants with a short vertical stem bearing a compact rosette of leaves, the lowermost of which lie flat on the substrate. Leaves entire, those of species whose rosettes are submersed mostly flat, those of terrestrial forms with their sides rolled upward, usually progressively more so toward the tips so that such leaves have a V-shaped outline. Some species, at least, produce buds from the leaves in the latter part of the growing season, these in turn forming new rosettes so that in such forms one often sees, the following season, clusters of rosettes. Flowers produced early in the growing season, each borne singly at the end of an elongate non-bracteate peduncle or scape; each rosette usually producing several flowers but these not all reaching anthesis at once. Glandular hairs, presumably associated with a carnivorous function, occur on the upper leaf surfaces, the scapes, the outer surface of the calyx, to a lesser extent on the outer surface of the corolla tube, and on the ovulary. The glandular secretions impart a greasy character to the surfaces, especially of the leaves. Flowers bisexual, hypogynous, gamopetalous, and 5-merous as to perianth. Calyx two-lipped, the upper lip with three lobes distinct nearly to the base, the lobes closely embracing the upper part of the corolla tube on only one side; the lower lip two-lobed, the lobes not usually incised more than half-way of the calyx and these embrace the lowermost portion of the corolla tube on the same side, the base of the spur extending flush from between the sinus of the lower lip of the calyx. Corolla more or less cylindric-tubular at base, lowermost portion of the tube rather abruptly contracted into a spur; above the tube the corolla flares, bearing five spreading lobes each of which is notched or incised. Corolla attached about midway of the tube and on one side, (the side embraced by the calyx), this part of the tube somewhat inflated, the sexual parts

seated within it at this point (Fig. 1d). From the lower side of the corolla tube just within the throat, projects a hairy palate, in most species extending obliquely outward from the throat, or (in one of ours) included within the throat. Hairs of the palate, of the ridge on the lower side of the corolla tube within and behind the palate, and on the inner side-walls of the tube are more or less characteristic for each species. Androecium comprised of two stamens; filaments thick and stout, arising immediately adjacent to each other on the upper wall of the corolla tube, then arching outward and upward along one side of the ovulary, curving inward again, the anthers nearly meeting and the whole androecium almost outlining a circle through which one side of the ovulary is visible (Fig. 3d). Ovulary subspherical, bearing at its summit two very unequal stigmatic lobes, the lower, larger, nearly orbicular lobe curving downward like a hood and completely or nearly covering the anthers; lower surface of the large lobe of the stigma abundantly clothed with sticky hairs to which the pollen clings. Ovulary 1-locular, with a bulbous free central placenta bearing numerous ovules (Fig. 1d). Fruit a 2-valved capsule. Seeds small, numerous, brown, their surfaces honeycombed.

KEY TO THE SPECIES OF SOUTHEASTERN PINGUICULA

(Constructed especially for living plants)

1. Expanded corolla not, or rarely, exceeding 1.5 cm across; palate not exserted from the throat of the corolla; rosettes rarely exceeding 3 cm broad ..... *P. pumila*
1. Expanded corolla 1.8 cm across or more; palate markedly exserted from the throat of the corolla; rosettes 5 cm broad or more.
   2. Flowers sulphur-yellow or golden-yellow ..... *P. lutea*
   2. Flowers violet to white.
      3. Pubescence on the lowermost portion of the scape consisting of elongated, pointed, multiceullular, non-glandular hairs; that of the uppermost portion comprised of 1-celled glandular hairs (transition from one to the other very gradual); expanded portion of the corolla veiny, usually markedly so ..... *P. caerulea*
      3. Pubescence of the scape uniform throughout its length and all glandular; expanded portion of the corolla not at all veiny.
         4. Leaves dull red or reddish-green; lobes of the corolla deeply incised ..... *P. planifolia*
         4. Leaves bright green (although sometimes drying reddish); lobes of the corolla merely notched.
            5. Lobes of the corolla as broad as long or broader; outer 3/4 of the corolla wisteria-violet and with a ring of white above the throat; corolla tube yellow, with reddish-brown veins; trichomes on the inner side walls of the corolla tube yellow ..... *P. primuliflora*
            5. Lobes of the corolla longer than broad; uniformly violet to white (no ring of white above the throat), deeper violet in the throat; corolla tube violet, with darker violet veins; trichomes on the inner side wall of the corolla tube white ..... *P. ionantha*

1. *Pinguicula pumila* Michx., Fl. Bor.-Am. 1:11. 1803. Fig. 1.

Rosettes mostly not exceeding 3-4 cm across. Leaves light-green to olive-green, ovate-oblong, the sides rolling markedly upward from just above the base, more so progressively toward the tip thus forming a V-shaped outline, the tips of the leaves mostly turning downward. Upper leaf surfaces glandular pubescent and with some longer non-glandular hairs on either side of the sunken midrib near the leaf base, these hairs directed across the midrib, crisscrossing each other.

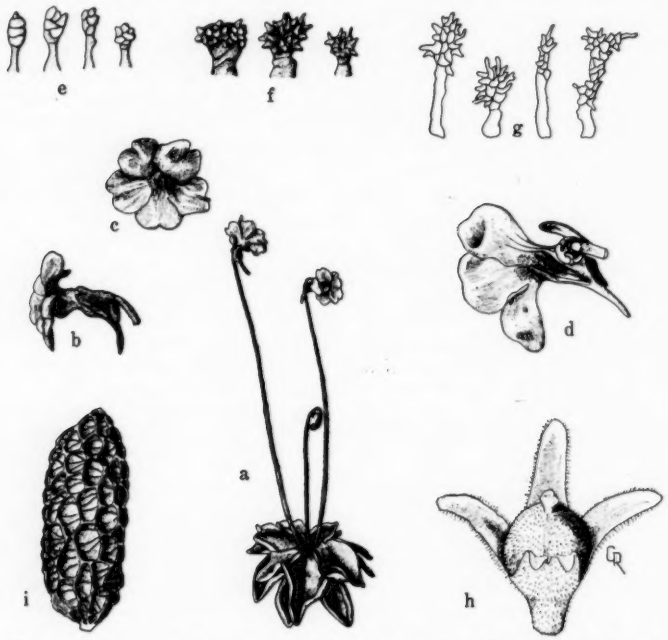


Fig. 1.—*Pinguicula pumila*: a, habitat; b and c, flower, lateral and face view; d, flower, longitudinal section; e, trichomes from palate; f, trichomes from ridge on corolla behind the palate; g, trichomes from inner walls of the corolla tube; h, capsule; i, seed.

Scapes to about 10 cm tall. Lobes of the upper lip of the calyx linear-oblong, blunt, about 3 mm long, those of the lower lip triangular, about 1.5 mm long, olive-green to dull-red. Corollas mostly 1.3-1.5 cm across, the lobes obovate, emarginate, violet to pale violet to white, rarely yellow; corolla tube violet, or yellow, violet mostly only in the deeper violet flowers, faintly to prominently reddish-brown veined; spur dull purplish-brown in the more deeply violet flowers, varying to yellow, veined or not, mostly 3-5 mm long, nearly linear. Palate sulphur-yellow, about 2 mm long, not exserted

from the throat of the corolla tube, clothed with short, stubby, or slightly irregularly knobbed yellow hairs; hairs on the inner ridge of the tube below the palate chrome-yellow to red, with short, stout stalks and knobby tips with very irregular surfaces; hairs on the walls of the tube yellow, more slender, but with very irregularly knobby tips. Filaments white, anthers and pollen very pale yellow or white. Stigma violet to white. Capsule 4-5 mm in diameter. Seed oblong to obpyramidal, mostly ca. 0.3-0.4 mm long, the alveolae mostly with 2-3 cross lines.

Moist, sandy soil, pine flatwoods and savannas. Southeastern North Carolina to the Florida Keys and Bahamas, westward to Louisiana and eastern Texas.

2. *Pinguicula lutea* Walt., Fl. Carol. 63. 1788. Fig. 2.

Rosettes to about 15 cm broad. Leaves yellowish-green, ovate to oblong, the sides rolled upward beginning about 1/3 of the distance from the base, increasingly more so toward the tips until the edges meet, thus the tips have an apparent acuminate tip owing to the curling. Leaves ciliate on the margins near the base, their upper surfaces glandular pubescent, with a few longer non-glandular hairs near the midrib toward the base. Scapes mostly 15-25 cm tall. Lobes of the upper lip of the calyx oblong, broadly rounded at their tips, about 6 mm long, those of the lower lip ovate-triangular, broadly rounded at their tips, about 3 mm long. Corollas mostly 2.5-3.5 cm across, the lobes broader than long, notched or divided to about 1/3 their length, the edges of the lobes smooth to irregular, or occasionally each lobe irregularly 2-3 sub-lobed or toothed. Expanded portion of the corolla sulphur-yellow, not veined, the tube greenish-yellow, usually conspicuously purplish veined on the lower side; spur slender, tapering, 5-10 mm long. Palate yellow, stout, blunt, well exserted from the throat, bearing abundant slender, yellow hairs with slightly enlarged clublike tips; hairs on the inner ridge of the tube, below the palate, with slender stalks and chrome-yellow to orange-red clublike tips having very irregular surfaces; hairs on the walls of the tube yellow, somewhat more slender, with less irregular clublike tips. Filaments white, anthers pale yellow, pollen white. Stigma yellow on the center of the larger lobe, grading to white on the edges. Capsule 7-8 mm in diameter. Seeds mostly oblong, 0.5-0.8 mm long, the alveolae with 3-4 cross lines.

Moist to wet sandy-peaty soils of seepage bogs, pine flatwoods and savannas. Southeastern North Carolina to Lake Okeechobee, Florida, westward to eastern Louisiana, on the coastal plain.

3. *Pinguicula caerulea* Walt., Fl. Carol. 63. 1788. Fig. 3.

Rosettes mostly 5-10 cm across. Leaves yellowish-green, ovate-oblong, their sides curling upward from just above the base, progressively more so toward their tips thus forming a V-shaped outline, the tips of the leaves turned downward. Leaves glandular pubescent above and with some long non-glandular hairs near the base on

either side of the sunken midrib, these directed across the midrib, criss-crossing each other. Scapes to about 20 cm tall, densely pubescent, the lower 1/3 portion with long, spreading, pointed, multicellular hairs. Upwards very gradually appear short, 1-celled hairs which produce a bulbous droplet of exudate on their tips. The long hairs very gradually diminish in number up the scape, the short ones become more numerous, the upper part of the scape having only the

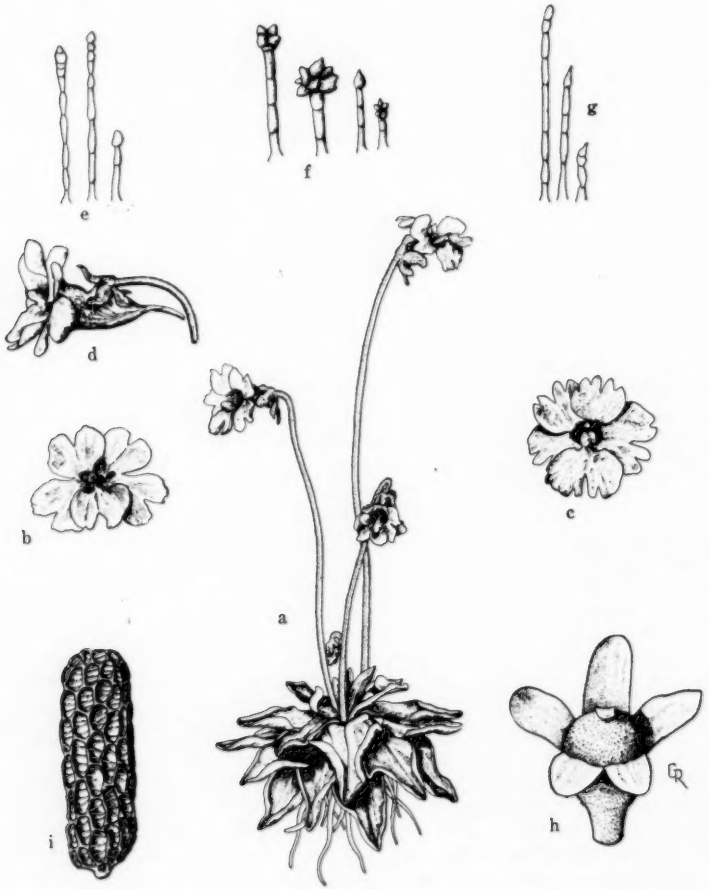


Fig. 2.—*Pinguicula lutea*: a, habit; b and c, two flowers, face view; d, flower, lateral view; e, trichomes from the palate; f, trichomes from ridge of corolla tube behind the palate; g, trichomes from the inner walls of the corolla tube; h, capsule; i, seed.

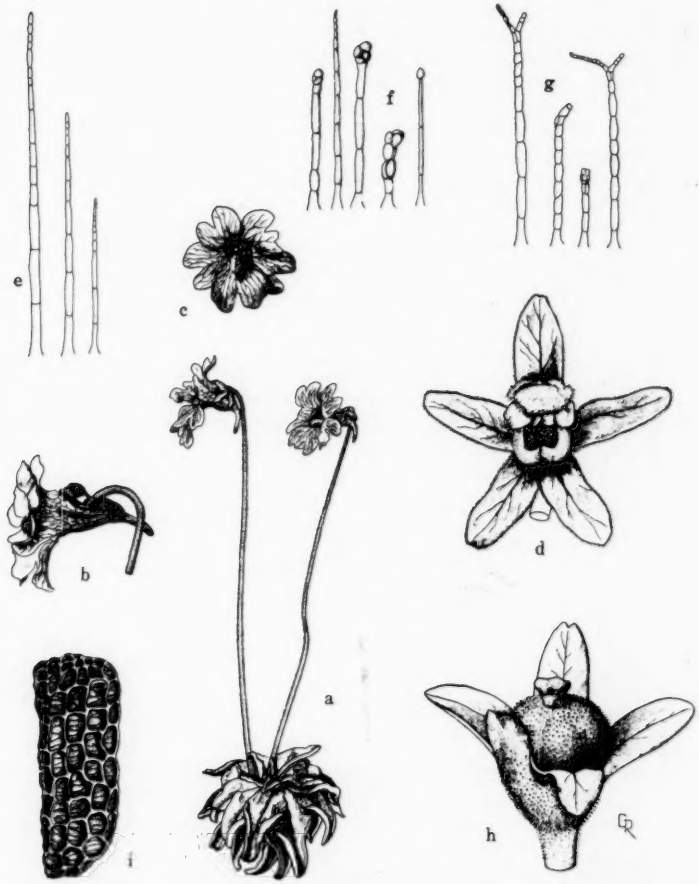


Fig. 3.—*Pingicula caerulea*: a, habit; b and c, flower, lateral and face view; d, face view of flower with corolla removed; e, trichomes from the palate; f, trichomes from ridge of the corolla behind the palate; g, trichomes from the inner walls of the corolla tube; h, capsule; i, seed.

latter. Lobes of the upper lip of the calyx linear-oblong, about 8 mm long, those of the lower lip lance-triangular or lanceolate, about 5 mm long. Corollas mostly 2.5-3.0 cm across, the lobes cleft from 1/3 to 1/2 their length, the subdivisions mostly broadly rounded, sometimes sub-notched or lobed. Expanded portion of the corolla varying from deep violet to pale violet, usually prominently veined, the veins deeper colored than the ground color, sometimes faintly veined.

Corolla tube and spur violet to greenish-yellow, distinctly violet-veined. Spur mostly 5-7 mm long, somewhat tapering. Palate broad and blunt, exserted from the throat, greenish-yellow to cream-colored, abundantly clothed with long, slender, essentially pointed hairs. Hairs on the ridge of the tube within and on the walls of the tube essentially like those of the palate, with barely enlarged tips, or with somewhat branched tips. Filaments white, anthers very pale yellow, pollen pale yellow or white. Larger lobe of the stigma tinted yellow in the center, white nearer the margins. Capsule ca. 1 cm in

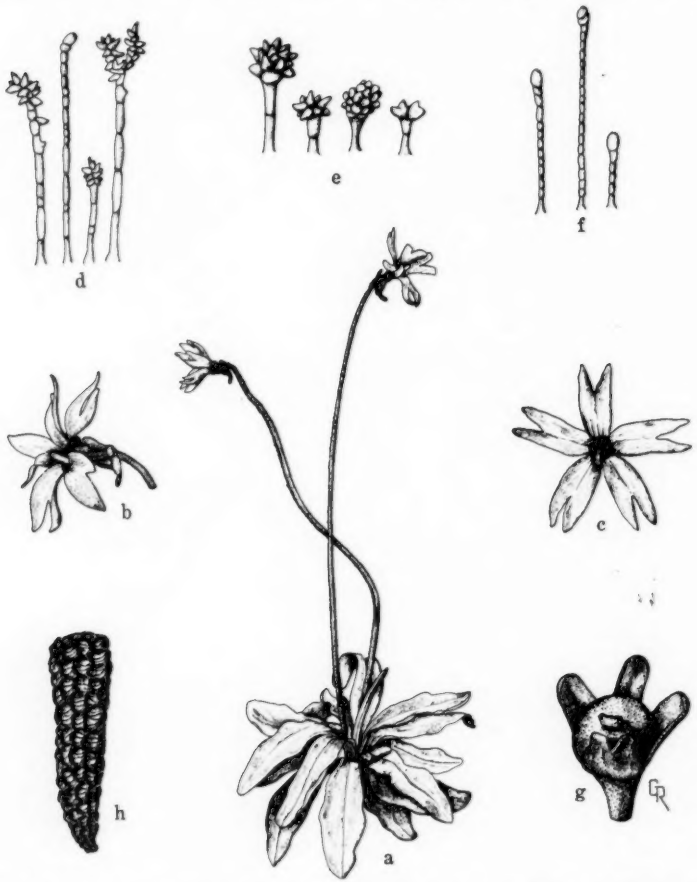


Fig. 4.—*Pinguicula planifolia*: a, habit; b and c, flower, lateral view and face view; d, trichomes from inner walls of tube; e, trichomes from ridge of tube behind palate; f, trichomes from palate; g, capsule; h, seed.

diameter. Seeds oblong or obpyramidal, mostly ca. 0.5 mm long, the alveolae with 3-4 cross lines.

Moist to wet sandy and sandy-peaty soils of pine flatwoods and savannas, southeastern North Carolina to Lake Okeechobee, Florida, westward to about the Apalachicola River, Florida, on the outer coastal plain.

4. *Pinguicula planifolia* Chapm., Fl. Southern U.S. ed. 3, 303. 1897. Fig. 4.

Rosettes to about 15 cm across. Leaves oblong, elliptic, or oblanceolate, thin and translucent, flat when fully developed, dull green and slightly to uniformly suffused with a dull purplish-red pigment. Upper leaf surfaces with very short glandular hairs. Scapes relatively slender, to 25 cm high, sparsely glandular pubescent below, more densely so near the summit. Calyx olive-brown or reddish-olive, the lobes of the upper lip oblong, about 4 mm long, those of the lower ovate-triangular, about 1 mm long, all rounded at their tips. Expanded portion of the corolla about 3 cm across, the lobes violet to almost magenta, occasionally nearly white, the throat deeper violet. Corolla lobes incised nearly 1/2 their length, lanceolate. Corolla tube somewhat veined. Spur oblong, 3-4 mm long, color of the calyx. Palate 4-6 mm long, exserted from the tube, slender, oblong, densely clothed with slender, yellow hairs with smooth to slightly irregularly surfaced clublike tips; hairs of the ridge of the corolla tube within and below the palate with sessile or very short-stalked, druselike hairs, yellow to orange or orange-red in color. Hairs on the wall of the tube within slender, stalked, white, and with smooth to very irregular clublike tips. Filaments pale to deep violet, anthers pale yellow, pollen white. Larger lobe of the stigma deep violet. Capsule ca. 5 mm in diameter. Seed obpyramidal, ca. 6-7 mm long, the alveolae with 2-4 cross lines.

In shallow water, margins of flatwoods ponds, depressions in flatwoods, ditches and shallow drainage canals. Leon, Liberty, Franklin, Gulf, Bay, and Walton counties, Florida, and near Ocean Springs, Mississippi.

5. *Pinguicula primuliflora* Wood and Godfrey, Rhodora 59:219-221. 1957. Fig. 5.

Rosettes to about 15 cm broad. Leaves bright green, more or less oblong, fully developed ones essentially flat, the upper surfaces with short glandular hairs. Scapes rather sparsely glandular pubescent, mostly 8-15 cm tall. Lobes of the upper lip of the calyx 5-6 mm long, broadly ovate-oblong, the lower about 3 mm long, broadly ovate-triangular, all rounded at their tips, dark olive-green, sometimes suffused with a little reddish pigment. Expanded corollas 2.5 - 3.0 cm across, the lobes obovate to sub-orbicular, broader than long, shallowly notched. Open face of the corolla wisteria-violet and with a ring of white just at the base of the lobes and above the

yellow throat, not veined. Corolla tube chrome-yellow, especially within, and prominently reddish-brown veined. Palate chrome-yellow, exserted, cylindrical, 4-5 mm long, densely clothed with clublike yellow hairs. Ridge of the corolla tube behind the palate bearing stout, short-stalked hairs with obovoid or mitten-shaped orange to

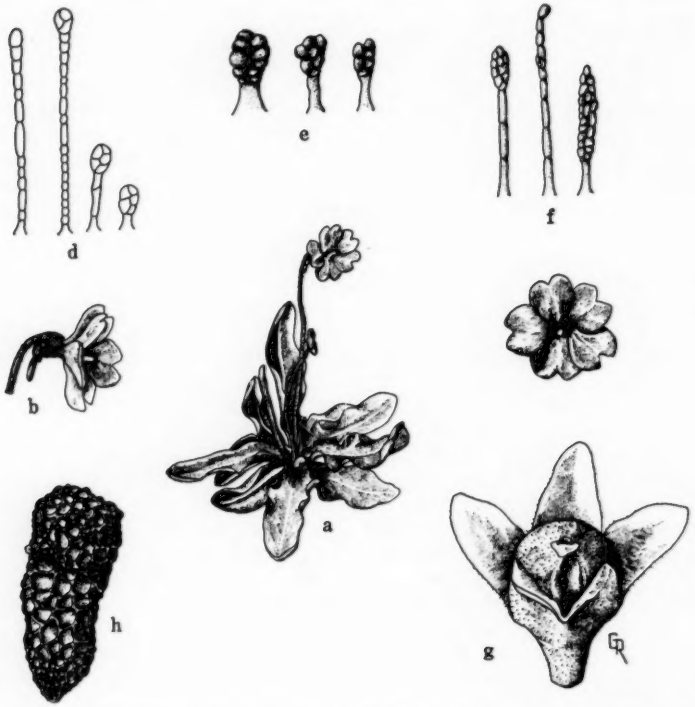


Fig. 5.—*Pinguicula primuliflora*: a, habit; b and c, flower, lateral and face view; d, trichomes from palate; e, trichomes from ridge of corolla behind palate; f, trichomes from inner walls of corolla tube; g, capsule; h, seed.

orange-red tips. Walls of the tube with chrome-yellow, slender, clublike hairs. Filaments white, anthers very pale yellow, pollen very pale yellow to white. Larger lobe of the stigma white. Capsule depressed-globose, about 5 mm in diameter. Seeds 0.5-0.7 mm long, obpyramidal to sub cylindric-truncate, the alveolae without cross lines.

In shallow flowing water of springy areas, along small streams, in shallow flowing water of ditches, commonly in dense to open shade. Present records are from the western part of the Florida

Panhandle, Early County, Georgia, and southern Alabama and Mississippi. Earlier records from Franklin and Liberty counties, Florida, were in error.

6. **Pinguicula ionantha** Godfrey, sp. nov. Fig. 6.

Folia laetevirentia spathulata plana usque 4-8 cm longa 2.0-2.5 cm lata. Scapi plerumque 10-25 cm alti parce breviterque glanduloso-pubescentes. Calycis lobi atroolivacei plerumque plus minusve purpurascentes; labium superius cum lobis oblongis rotundatis circa 4 mm longis, inerius cum lobis ovato-triangularibus obtusis 3 mm longis. Corolla circa 2 cm lata cum lobis pallide violaceis vel albis obovatis leviter emarginatis 7-9 mm longis 6-7 mm latis; tubo 5 mm longo, cum pauce plus saturate violaceo et venoso; palato conico vel anguste cylindrico 4-6 mm longo exserto; calcare 4-5 mm longo lineari-cylindrico flavo vel olivaceo. Stigmatis lobus inferior violaceis. Capsula depresso-globosa 5 mm diametro. Semina oblongo-cylindrica brunnea 0.6-0.8 mm longa apice truncata vel oblique truncata; alveolae transverse 1-2 lineatae.

Holotype.—Franklin County, Florida: shallow water, depression in flatwoods, 11 miles S of Sumatra; with *P. planifolia;* March 26, 1960, *Godfrey 59362* (deposited in the Gray Herbarium).

Additional specimens.—FLORIDA. *Franklin County*: in shallow water of broad drainage ditch bordering pine flatwoods, 3 miles N. of Carrabelle, March 18, 1960, *Godfrey 59343; Liberty County*: boggy margins of drainage ditch through pine flatwoods, 8 miles S of Telogia, March 26, 1960, *Godfrey 59363; Gulf County*: shallow water, depressions in flatwoods, 6.5 miles S of Wewahitchka, with *P. planifolia,* March 26, 1960, *Godfrey 59361; Bay County*: deep quagmire bog, ca. 11 miles E of Panama City, between Panama City and Wewahitchka, shallow surface water on bog, April 8, 1960, *Godfrey 59390.*

The following two collections were previously assigned to *P. primuliflora* (Wood and Godfrey, 1957). *Franklin County*: common on moist sands of shrub bog-savanna, 15 miles NE of Eastpoint, February 9, 1957, *Kral 4037a; Liberty County*: several plants on wet sands along margin of railroad ditch, shrub slash pine bog, 6 miles N of Vilas, Feb. 26, 1956, *Kral 1960 and Godfrey.*

Rosettes to about 15 cm across. Leaves bright green, oblong, rounded at their tips, essentially flat when fully developed, with just the edges rolled upward, the upper surface clothed with short glandular hairs. Scapes mostly 10-15 cm tall, rather sparsely short-glandular pubescent. Upper lip of the calyx with oblong, rounded lobes about 4 mm long, those of the lower ovate-triangular, obtuse, 3 mm long, all dark olive-green and usually suffused with some purplish pigment. Expanded corollas mostly about 2 cm across, the lobes obovate, shallowly notched, longer than broad, pale violet to white. Throat of the corolla and the tube deeper violet than the limb and with darker violet veins. Spur 4-5 mm long, yellow to olive, linear-cylindric. Palate 4-6 mm long, exserted from the throat,

conical or narrowly cylindric, the upper 2/3 yellow and clothed with yellow, slender clublike hairs some of whose tips turn red as they age; lower 1/3 of the palate on the upper side violet like the throat and bearing few or no hairs, hairy to the base on the lower side. Ridge

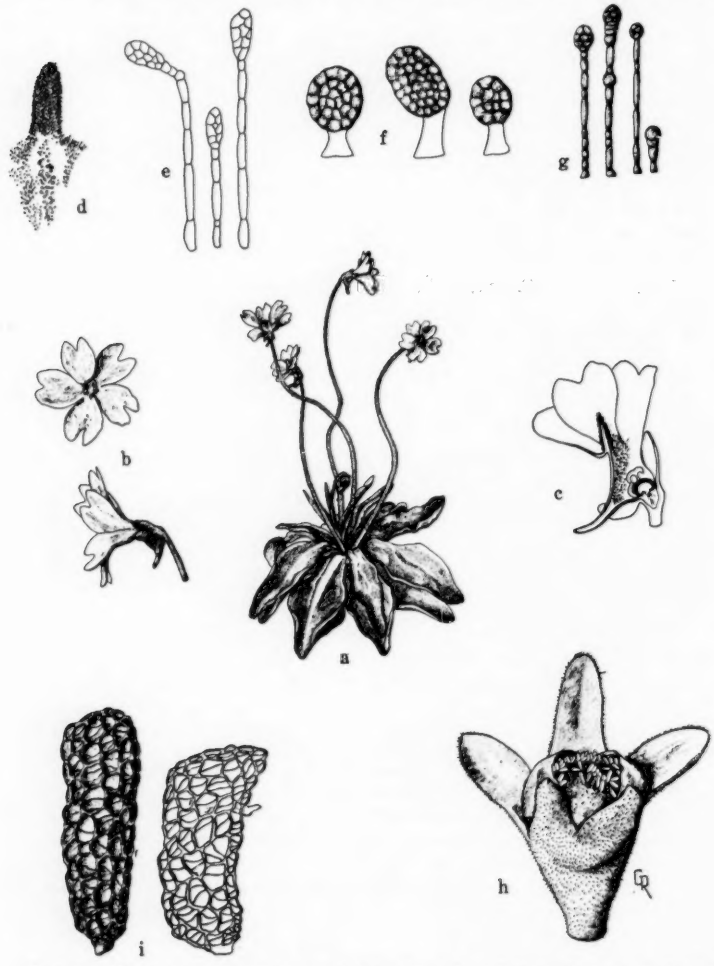


Fig. 6.—*Pinguicula ionantha*: a, habit; b and c, flower, face view, lateral view, longitudinal section; d, pubescence on palate, ridge of tube behind palate, and on inner walls of tube; e, trichomes from palate; f, trichomes from ridge of tube behind palate; g, trichomes from inner wall of corolla tube; h, dehiscing capsule; i, seeds.

of the corolla tube within and below the palate with relatively distant hairs having short, stout stalks and spherical to broadly oblong, orange to orange-red tips. Walls of the tube with relatively few, white, club-like hairs. Filaments pale violet to white, anthers and pollen very pale yellow. Larger lobe of the stigma violet to pale violet. Capsule

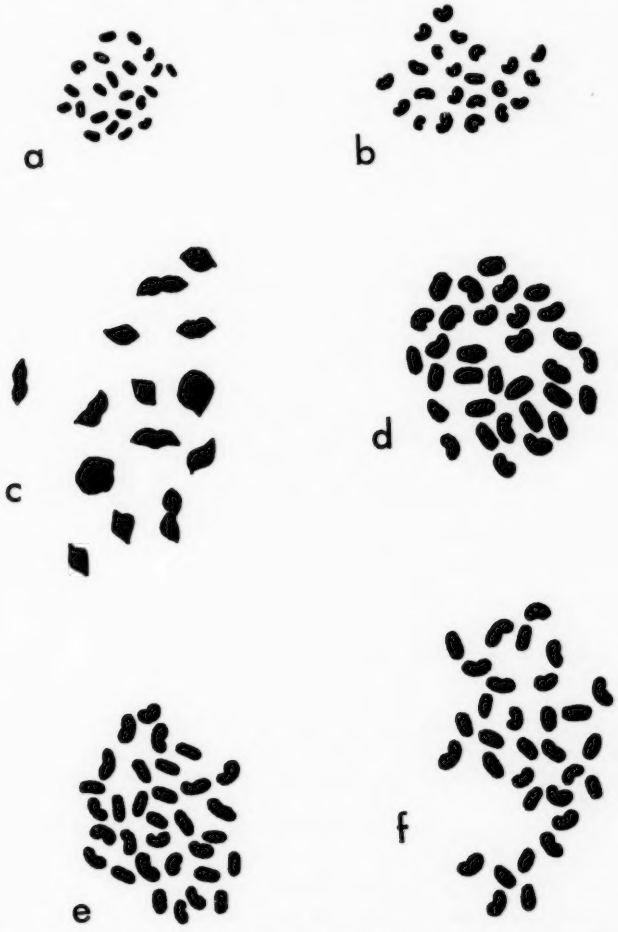


Fig. 7.—Camera lucida drawings of mitotic (except "c" which is meiotic) chromosomes, all approximately X 2800: a, *P. pumila* (2n = 22); b, *P. ionantha* (2n = 22); c, *P. caerulea* (n = 16, twelve bivalents and two quadrivalents); d, *P. planifolia* (2n = 32); e, *P. primuliflora* (2n = 32); f, *P. lutea* (2n = 32).

depressed-globose, about 5 mm in diameter. Seed oblong-cylindric to obpyramidal, the alveolae with 1-2 cross lines.

In flatwoods depressions, ditches, and shallow drainage canals, and bogs, the rosettes mostly submersed (at least when conditions are most favorable); occasional plants, or in occasional places all plants occur in mucky soil bordering such areas. Frequently intermixed with *Pinguicula planifolia*. Liberty, Franklin, Gulf and Bay counties, Florida.

The relatively flat leaves of *Pinguicula ionantha* are very much like those of both *P. planifolia* and *P. primuliflora* in form and contrast with those of the other more terrestrial species the leaves of which curl upward markedly from somewhat above the leaf bases and toward the tips. The leaves of *P. planifolia* are suffused with a dull purplish-red pigment, however, while those of *P. ionantha* are bright green as are those of *P. primuliflora*. The latter two are not known to occur even in the same general area whereas *P. planifolia* and *P. ionantha* commonly occur together. The distinguishing combination of features of *P. ionantha* does not suggest a hybrid origin. This combination of features includes the pattern of coloration of the corolla as well as the actual colors, the characteristic hairs of the tip of the palate and the interior of the corolla tube, the near lack of hairs on the base of the upper surface of the palate, the shape of the corolla lobes, and the cross lines in the alveolae of the seed surfaces. Although *P. ionantha* has some morphological features and habitat "preferences" suggesting affinity with *P. planifolia* and *P. primuliflora*, its chromosome number, $2n = 22$, is the same as that of *P. pumila* whereas the number for all the other four species of our area is $2n = 32$. (See below).

CHROMOSOMES

Chromosome numbers reported previously for the genus were briefly reviewed by Wood and Godfrey (1957). These included the following: $2n=16$ (*P. villosa* L.); $2n=32$ (*P. alpina* L.); $2n=44$ ("*P. caudata*"); $2n=64$ (*P. grandiflora* Lam., *P. vulgaris* L.). The chromosome numbers for the species here treated are listed below together with the vouchers deposited in the herbarium of Florida State University:

a. *P. pumila*: $2n=22$, *Godfrey 60547, 60548, and Stripling 983.*
b. *P. ionantha*: $2n=22$, *Godfrey 60552, 60534.*
c. *P. caerulea*: $2n=32$, *Godfrey 60542.*
d. *P. planifolia*: $2n=32$, *Godfrey 60533, 60551.*
e. *P. primuliflora*: $2n=32$, *Godfrey 60532 and Tyson*, March 3, 1961.
f. *P. lutea*: $2n=32$, *Godfrey 60535, 60550.*

Chromosome counts were made from immature buds. The buds were fixed in a solution of 5 parts absolute alcohol:3 parts chloroform:1 part glacial acetic acid. Counts were made from iron-aceto-carmine squashes. See Figure 7 for camera lucida drawings of the chromosomes of each species.

REFERENCES

BARNHART, J. H. 1915. Segregation of genera in Lentibulariaceae. *Mem. N. Y. Bot. Gard.*, **6**:46-47.

WOOD, C. E., JR. AND R. K. GODFREY. 1957. *Pinguicula* (Lentibulariaceae) in the southeastern United States. *Rhodora*, **59**:217-230.

Morphological Variation Between Local Populations of Taricha granulosa in Oregon

ROBERT L. LIVEZEY and GILBERT A. WYLLIE[1]
Sacramento State College, Sacramento, California

For the past twenty years *T. granulosa* has been considered to represent the stock from which all West-coast forms of *Taricha* arose (Twitty 1942, Riemer 1958). If so, there should be much variation between local populations of this species. The extent of variation has not been detected because specimens from several localities have been combined into a single sample, studies have dealt with a single locality, or only incidentally approach the problem of variation.

This study demonstrates the extent of variation to be expected in common characters within and between areas of a normal part of the range. "Local population" refers to a sample from a single breeding locality. Our method satisfies three requirements: that individuals in each local population be in close contact to assure freedom of gene flow; that distances between collecting sites be great enough to permit morphologic differentiation; that specimens have well developed morphologic characters.

Materials and Methods

Collection sites.—During 1952 the senior author collected samples from the following localities: (a) Artificial pond, 300 feet above sea level, on the south slope of Coffin Butte, nine miles north of Corvallis, Benton County. At the time of collecting, June 18, draining operations concentrated the newts in the outlet. The 115 individuals taken probably represented slightly less than one-half the total. Grasses and scattered shrubs surrounded the pond, the bottom of which was black muck resulting from the decay of the dense growth of aquatic plants in and around the edge. (b) On June 21 a collection of 74 specimens was made at Frog Lake, U. S. Highway 26 at Wapinitia Pass, Wasco County, at an elevation of 3800 feet. This small lake is in the typical coniferous forest of the Cascade Mountains. As with the Coffin Butte pond, the bottom of Frog Lake was dark colored as a result of the soil conditions and decayed vegetation; however, the substrate in the lake was much firmer and lightly covered with conifer needles, twigs, and branches. Much of the lake was shaded by numerous trees growing in the shallow water at the edge. (c) During the evening of June 21 a collection of 23 individuals was made at the Crown-Zellerbach mill pond, 400 feet in elevation, two and one-half miles southeast of Molalla, Clackamas County. The area surrounding the pond

[1] Present address: Biology Dept., Purdue University, Lafayette, Ind.

was similar to that around the Coffin Butte pond; however, the Molalla pond had little vegetation and a light colored bottom of tan clay.

It is 46 airline miles from Coffin Butte to Molalla and 41 from Molalla to Frog Lake. Both Coffin Butte and Molalla are in the lower portion of the Willamette River drainage system, while Frog Lake is just to the east of the low crest of the Cascade Range and drains into the Deschutes River via the White River on the east slope of the Cascades. However, Frog Lake, being located at Wapinitia Pass, is only one mile from the Salmon River, which flows down the west slope.

Treatment of the specimens.—Field notes were taken on the color, general appearance, and habitat. Specimens were relaxed in tricaine methanesulfonate (M.S.222), fixed in 10% and preserved in 5% formalin. Immediately after returning to the laboratory measurements were made with a vernier caliper. To avoid the use of juveniles, all specimens with a snout-vent length less than 50 mm were omitted.

Morphologic measurements were made according to standard methods, except for the following: snout-vent length was taken from tip of snout to posterior extent of vent opening, head length from tip of snout to posterior margin of jaw, and nostril-eye distance from posterior margin of nostril to anterior corner of eye.

RESULTS AND DISCUSSION

Coloration.—In life the color of the three populations was noticeably different. Animals from Coffin Butte were dark brown dorsally with yellowish-orange venters and more nearly represented the coloration of *T. granulosa* usually noted. All specimens seen or collected at Molalla were unusually light colored. Dorsal pigmentation was consistently a light milk-chocolate brown. The venters were lemon-yellow with practically no trace of orange. This light hue was in keeping with the light tan color of the pond substrate and surroundings. Individuals at Frog Lake had a dark, blackish-brown dorsal color which blended with the dark substrate. Ventral coloration was a rich reddish-orange, bearing a resemblance to the pigmentation of *T. rivularis*.

Arbitrary classes were established for extent of dorsal color on sides, sharpness of dorsal-ventral color demarcation, and extent of ventral color on the tail. For extent of dorsal color on sides three classes were used: 1 = pigment extended ventrally to about the ventral insertion of the limbs; 2 = pigment came to only slightly below the dorsal insertion of the limbs; 3 = pigment did not reach the level of the limb insertions. Animals from Coffin Butte had 23% class 1, 70% class 2, and 7% class 3; those from Molalla were 39% class 1, 57% class 2, and 4% class 3; the Frog Lake sample was 55% class 1, 45% class 2, and 0% class 3. Dorsal pigmentation was therefore more extensive on individuals of the Frog Lake population.

Three classes were used to denote sharpness of the boundary

between dorsal and ventral pigments: 1 = very sharp demarcation (no melanin grading into ventral pigment), 2 = moderate amount of melanin grading into ventral pigment, 3 = line of demarcation indistinct (considerable melanin grading into ventral pigment). Results for this character were: Coffin Butte 71% class 1, 15% class 2, and 14% class 3; Molalla 26% class 1, 35% class 2, and 39% class 3; Frog Lake 74% class 1, 12% class 2, and 14% class 3. The Molalla population had the greatest degree of melanic suffusion into the ventral color.

For extent of the ventral color on the tail it was necessary to establish five categories: 1 = ventral color from vent entirely to tail tip, 2 = color almost to tip, 3 = color three-quarters of distance from vent to tip, 4 = color one-half the tail length, and 5 = color one-quarter or less. Results for this character were: Coffin Butte 7% class 1, 54% class 2, 37% class 3, 1% class 4, and 1% class 5; Molalla 48% class 1, 43% class 2, 9% class 3, and 0% classes 4 and 5; Frog Lake 12% class 1, 26% class 2, 33% class 3, 29% class 4, and 0% class 5. The Molalla group was distinctive in that ventral pigmentation was more extensive.

Examination of the extent of the melanistic band on the cloacal lips showed that this character was too variable within each local population to be of value in a comparison between populations. Most specimens possessed an incomplete band extending about halfway down the lips, but there was a range from complete absence to complete development.

Riemer (1958) in treating the melanic pigment on the snout of *Taricha* set up nine arbitrary classes. We used only three, but these can be compared reasonably well to figure 15 in Riemer's analysis: 1 = snout pigmented, 2 = snout moderately light, and 3 = snout decidedly light. Coffin Butte specimens were 46% class 1, 51% class 2, and 3% class 3. Molalla individuals were 0% class 1, 65% class 2, and 35% class 3. Frog Lake animals were 51% class 1, 46% class 2, and 3% class 3. These data further bear out the noticeable difference in pigmentation of the Molalla population from that of the other two samples.

Extreme variation exists in pigment distribution and intensity both within and between local populations. Each local population has its own coloration seemingly adjusted to the local conditions. However, overlap is such that one population could be considered preadapted to the conditions of either of the others.

Gular fold.—The gular fold, also highly variable, ranged from very weak to strongly developed, that of the Molalla population being the most pronounced.

Palatine teeth.—The pattern formed by the two rows of palatine teeth had been considered as a rather consistent character for *T. granulosa*. This configuration, closely resembling an inverted V, does vary. Of the specimens examined the range was from the typical inverted V to a pattern resembling an inverted Y. Configurations were ob-

served which fit the patterns for all species of *Taricha* as illustrated by Twitty (1935). Variation might involve the anterior or posterior half of the teeth rows or it might involve the right or left side of the pattern. Among the Coffin Butte sample 11% did not possess the typical pattern, 30% of the Molalla sample were atypical, and 23% of the Frog Lake specimens were variable.

Relation of corneal surface to jaw margin.—For the Californian species of *Taricha,* Twitty (1942) states that in *T. granulosa* the jaw margin extends laterally below the eye, so that when viewed from above, the corneal surface of the eye is not visible in free profile. This is supposedly the result of a smaller eye and broader head than is the case with the other species. In the Oregon populations it was found convenient to set three classes of conditions to compare the samples. These were designated: — for those in which corneal surface did not reach the jaw margin, # for those in which corneal surface coincided with jaw margin, and + for those in which corneal surface extended beyond the jaw margin. It was found that no uniformity existed in the samples examined. Coffin Butte specimens more nearly approached the condition described by Twitty; the results were — 53.2%, # 15.9%, and + 30.9%. Molalla animals were — 4.3%, # 17.4% and + 78.3%. Frog Lake specimens were — 40.5% # 14.9%, and + 44.6% Most of Molalla and Frog Lake individuals had corneal surfaces either reaching or extending beyond the jaw margin. With 46.8% of the Coffin Butte specimens having corneal surfaces reaching or extending beyond the jaw margin, this character cannot be considered a reliable criterion for discrimination. In the Molalla sample the condition had reached an extreme (# and + 95.7%), which further set this population apart from the others.

Linear measurements.—The mean snout-vent length for the three populations varied only within 1.53 mm, the Molalla group being the largest with a mean of 72.13 mm and a range of 62 to 81 mm. Coffin Butte was the smallest with a mean of 70.6 mm, but the same range as the Molalla. The Frog Lake group contained the smallest and the largest individuals, showing a range of 59 to 85 mm with a mean of 71.76 mm. With respect to head width the mean varied 1.39 mm. Coffin Butte specimens showed the greatest range, 11.5 to 18.4 mm with a mean of 14.74 mm, and Molalla specimens had noticeably broader heads than the other two, with a mean of 16.13 mm and a range of 13.5 to 18.4 mm. The Frog Lake sample had a mean of 14.76 mm with a range of 13.0 to 16.9 mm. In head length the Molalla animals were the largest, having a mean of 19.65 mm with a range of 17.0 to 22.9 mm, the Frog Lake the smallest, with a mean of 16.18 mm and a range of 13.5 to 19.9 mm, and Coffin Butte the greatest range, 13.5 to 21.9 mm with a mean of 18.08 mm, although not the largest single individual. The mean for this character varied 3.47 mm between the populations.

The largest eye opening was possessed by the Frog Lake population, followed in decreasing order by the Coffin Butte and Molalla

groups. Variation of the means was within 0.66 mm. Means and ranges for this character were Coffin Butte 4.79 mm with 3.8 to 5.5 mm, Molalla 4.3 mm with 3.8 to 4.9 mm, and Frog Lake 4.96 mm with 4.2 to 5.9 mm. The Molalla population, with the smallest eye length and broadest head still had, as previously noted, the greatest percentage of individuals with corneal surface extending beyond the jaw margin. This is explainable by the fact that the eyes of these animals were nearer the periphery of the head as shown by the interorbital distance. Specimens from Molalla had the largest interorbital distance with a mean of 4.86 mm and range of 4.2 to 5.5 mm. Frog Lake was the smallest with a mean of 4.43 mm and range of 3.4 to 5.3 mm. The Coffin Butte sample had the greatest range, 3.6 to 6.3 mm, with a mean of 4.79 mm. The means for this measurement varied within 0.43 mm.

Correlated with the long wide head and small eyes, the Molalla group had the largest nostril-to-eye distance with a range of 3.2 to 4.7 mm and a mean of 3.98 mm. Coffin Butte and Frog Lake populations varied only 0.1 mm in their means. Coffin Butte had a mean of 3.7 mm and a range of 2.8 to 4.5 mm, while the Frog Lake mean was 3.8 mm with a range of 3.0 to 4.5 mm. Variation of means between the three populations was 0.18 mm.

These measurements indicate the decided variation to be expected within and between local populations of *T. granulosa*. It also becomes evident that the robust appearance of the Molalla population observed in the field represents a real difference in body proportions, particularly the massiveness of the head.

Analysis of ratios.—In this study each ratio was determined as a percentage by dividing the smaller measurement by the larger. All statistical calculations are summarized in Table I.

Lack of overlap between the standard errors of head length/snout-vent length indicate that three distinct populations were being examined. The smaller head of the Frog Lake individuals explains the more apparent separation of this group. With respect to head width/head length the Frog Lake population was even more distinct. It again appears to be the result of the smaller head width of these animals. Coffin Butte and Molalla samples, however, were not significantly distinct. It will be noted that the Frog Lake population also spans 88% of the total observed range. Eye length/interorbital distance revealed the distinctness of the three local populations; there was nonoverlap of the standard errors, with an extensive observed range. Small eyes of the Molalla specimens and the smallest interorbital distance of the Frog Lake sample explains their respective low and high extremes.

Eye length/head length showed complete separation of the three local populations. As with the preceding ratios, the Frog Lake population had the greatest range. The extremes of the Molalla and Frog Lake individuals were the result of the respective small eyes and large eyes coupled with the large head length and small head

TABLE I.—Statistical analysis (all measurements are in millimeters)

Sample	No. of Specimens	Range	Mean	Standard Error	Standard Deviation	Variability Coefficient
Head Length to Snout-Vent Length						
Molalla	23	.26-.28	.27	.0020	.01	3.71
Coffin Butte	92	.23-.28	.25	.0010	.01	4.00
Frog Lake	73	.19-.27	.22	.0035	.03	13.63
Head Width to Head Length						
Molalla	23	.75-.88	.82	.0062	.03	3.66
Coffin Butte	92	.75-1.01	.81	.0041	.04	4.94
Frog Lake	73	.78-1.09	.93	.0081	.07	7.53
Eye Length to Interorbital Distance						
Molalla	23	.80-.98	.88	.0104	.05	5.68
Coffin Butte	92	.80-1.27	1.01	.0115	.11	10.89
Frog Lake	73	.88-1.37	1.13	.0128	.11	9.73
Eye Length to Head Length						
Molalla	23	.20-.25	.22	.0020	.01	4.54
Coffin Butte	92	.21-.35	.27	.0031	.03	11.11
Frog Lake	73	.21-.38	.31	.0035	.03	9.67
Eye Length to Nostril-Eye Distance						
Molalla	23	.96-1.32	1.08	.0166	.08	7.41
Coffin Butte	92	.98-1.64	1.31	.0135	.13	9.92
Frog Lake	73	1.09-1.67	1.31	.0128	.11	8.39
Interorbital Distance to Nostril-Eye Distance						
Molalla	23	1.08-1.46	1.23	.0208	.10	8.13
Coffin Butte	92	.98-1.72	1.30	.0135	.13	10.00
Frog Lake	73	.90-1.67	1.17	.0152	.13	11.11

length. Isolation of the Molalla sample as regards eye length/nostril-eye distance was also the effect of the small eyes. No significant difference was observed between the populations when interorbital distance/nostril-eye distance was examined. Range of variation was quite considerable in each population sample.

Ratios of head length/snout-vent length, eye length/interorbital distance, and eye length/head length showed all local populations to be statistically distinct from one another. Head width/head length further served to separate the Frog Lake specimens, while eye length/nostril-eye distance would distinguish the Molalla population. However, examination of standard deviation and range for these characters illustrates the great degree of variation to be expected within and between local populations of *T. granulosa*. The variable tendency of this species is also apparent by comparison of the values of the variability coefficient.

Discussion.—The foregoing data indicate the *T. granulosa* does demonstrate a considerable degree of variation between local popula-

tions. Whether the morphologic entities considered are distribution and intensity of pigment, linear measurements of anatomical parts, relationships of body parts, or degree of development of a selected character does not alter this conclusion. Differences between the three local populations examined are as marked as the differences summarized by Myers (1942) in delineating the subspecies *T. g. twittyi* and *T. g. similans*. This would support Riemer's (1958) conclusion that the species *T. granulosa* has only two subspecies (*T. g. granulosa* and *T. g. mazamae*) that are clearly recognizable. Several of the characters that have been used in the past as morphological criteria for separating the various species of the genus, can no longer be regarded valid. In fact, the extreme variation demonstrated among these three local populations might be interpreted as supportive for Pimentel's (1960) suggestion that the genus *Taricha* consists of only two species (*T. torosa* and *T. rivularis*) with the former being represented by two groups of closely related subspecies. Pimentel suggests that the forms *T. t. torosa* and *T. t. sierrae* belong to one subgroup and *T. g. granulosa* and *T. g. mazamae* to another.

Such variation between local populations of *T. granulosa* undoubtedly is the result of a combination of factors which need further investigation. Geographic mapping of the number and kinds of chromosomal inversions in selected areas of the range of *Taricha* should be enlightening. It is conceivable that the relative inability of these animals to travel any great distances, in a reasonably short time, would reduce gene flow from one local environment to another. The tendency of *Taricha* to return to its place of origin for breeding (Twitty, 1955) would also diminish gene flow between separate local populations. In a widespread form such as this, especially if it is a primitive and plastic stock, these conditions would encourage variation. Yet, through gene transfer from immediately adjacent populations there would be sufficient gene interaction throughout the geographic range to keep the species fundamentally similar in morphologic respects. Under such system the somewhat geographically separated local populations could become adapted to the immediate ecologic conditions, or allowed to express unswamped divergencies.

REFERENCES

MYERS, G. S. 1942. Notes on Pacific Coast *Triturus*. *Copeia*, **1942**(2):77-82.

PIMENTEL, R. A. 1960. Inter- and intrahabitat movement of the rough-skinned newt, *Taricha torosa granulosa* (Skilton). *Am. Midl. Nat.*, **63**(2): 470-496.

RIEMER, W. J. 1958. Variation and systematic relationships within the salamander genus *Taricha*. *Univ. Calif. Pubs. Zool.*, **56**(3):301-390.

TWITTY, V. C. 1935. Two new species of *Triturus* from California. *Copeia*, **1935**(2):73-80.

———1942. The species of California *Triturus*. *Ibid.*, **1942**(2):65-76.

———1955. Field experiments on the biology and genetic relationships of the Californian species of *Triturus*. *J. Exp. Zool.*, **129**(1):129-148.

Forest History of Martha's Vineyard, Massachusetts
I. Modern and Pre-Colonial Forests

J. GORDON OGDEN, III
Department of Botany and Bacteriology,
Ohio Wesleyan University, Delaware

ABSTRACT: Studies of forest history on the island of Martha's Vineyard, Massachusetts have included three main lines of investigation: a survey of the present vegetation; historical documents relating to colonial land use; and pollen-analytic investigation of postglacial lakes and bogs. Details of the postglacial vegetational and climatic history of the island are the subject of a separate paper. Some evidence from the pollen-stratigraphic studies are included in this paper.

The present vegetation of the Vineyard is in various stages of reforestation following clear cutting, farming, and pasturing. The dominant trees on the island at the present are: Oak, Pine, Beech, Gum, and Hickory. Old-field succession consists of the following stages: Juniper, Pine, Pine-Oak, Oak-Hickory-Beech.

From early historical documents it seems probable that hemlock and white pine were not present in the pre-colonial forests. Other forest trees not mentioned in the historical records of this area, nor found in pollen data include ash, basswood, tulip tree, and chestnut. Although fossil cones of white pine have been found on the Vineyard, pollen studies of the leaf litter associated with the pine cones show no evidence of European occupation at the time the pine cones were deposited.

There is no evidence to show that the early colonists found forests substantially different from those found in the area today. There is some evidence that the trees the colonists found may have been considerably larger with a high canopy.

INTRODUCTION

Although the vegetational history of southern New England has attracted the attention of botanists for many years, there is little agreement upon the nature of the pre-colonial forests. The evidence available, mostly in the form of old travel diaries, indicates that the colonists found forest conditions similar to those of today (Bromley, 1935, Nichols, 1935, Raup, 1937, 1940). Bromley (1935) attributed the open stands and the park-like character of the vegetation of repeated burning by the Indians. Raup (1937) rejected the idea of ". . . a wholesale conflagration in Massachusetts, Rhode Island, Connecticut, and southern New York as would involve most of the inflammable woods every year, or even every 10 or 20 years (as) inconceivable." Nevertheless, as Lutz (1928) pointed out, fire has been an extremely important factor in determining the composition of the modern forests. There is general agreement, however, that the predominant forest type was a "sprout hardwood" made up of white, red, and black oaks with hickories, tulip trees, and chestnut as an integral part of the association.

There are divergent views on the constitution of the climax, or virgin forests. Fisher (1933), Bromley (1935), and Nichols (1935)

thought that the climax forest for this region was a mixed timber of hemlock and northern hardwoods such as beech, sugar maple, and yellow birch. Their view is opposed by Raup (1937) who considers the "sprout hardwood" as a post-climax type dating from the post-glacial warmth maximum described by Sears (1932). Raup cites the trend toward cooler climates in the past 3000 years as one of the principal reasons for the apparent expansion of the white-pine-hemlock-northern hardwood forest types.

The vegetation of the offshore islands of southeastern New England has received little attention despite a long and richly documented colonial history. Hollick (1894) postulated a land connection between the coastal plain of New Jersey and the offshore islands and Cape Cod on floristic grounds. Fernald (1911) accepted this hypothesis as an explanation of the coastal plain relationships he observed in the floras of Newfoundland and Labrador. Floristic studies of Cape Cod and the offshore islands are restricted to Bicknell's (1919) survey of the vascular plants of Nantucket and a flora of the Elizabeth Islands by Fogg (1930). Despite the larger size and greater relief of the island of Martha's Vineyard, there are no comprehensive floras available. The writings of both Bicknell and Fogg include several references to Martha's Vineyard, in particular to the "more boreal" aspect of the plants of this island.

This discussion will be restricted to a brief survey of the present vegetation of Martha's Vineyard and to those documents and observations on the colonial and precolonial forests which have not received attention elsewhere.

Acknowledgments.—It is a distinct pleasure to recognize the assistance and support of the following individuals: Professor Paul B. Sears of Yale University, whose comments and suggestions in the field and in the laboratory were a great source of encouragement and inspiration; Professors H. J. Lutz and D. M. Smith of the Yale School of Forestry, for many helpful suggestions and the loan of field equipment.

Much of the field work in connection with this study was made possible by a grant-in-aid from the Society of the Sigma Xi and the Research Council of America. I should also like to recognize the encouragement and assistance of my wife, Anne Bowditch Ogden for her enthusiastic and able help in the field and in the laboratory.

Portions of this material were submitted to the Graduate School of Yale University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

LOCATION AND CLIMATE

Martha's Vineyard (Lat. 41°25′N., Long. 70°30′W.) is an island of approximately 100 square miles. It is the largest of a group of islands south and southwest of Cape Cod, Massachusetts. Physiographically, these islands and Cape Cod form the northernmost outposts of the Atlantic Coastal Plain which dips beneath the sea here and continues eastward as George's Bank. The surfaces of the islands

are of glacial drift and date from the retreat of the Wisconsin ice sheet. Several syntheses of the geological history of this area are available (Shaler, 1886; Woodworth and Wigglesworth, 1934; Flint, 1957).

The moraines which form the northwest coast of Martha's Vineyard have a maximum relief of 300 ft. Their topography is rolling and is in strong contrast to the flat and almost level outwash plain to the east. The soils are rocky, thin, and lack almost every soil component except sand. Successful truck farming is carried on in the "Great Plains," as the outwash plain is locally termed, but near the moraines only pasture farming is practiced because of the rocky soil.

TABLE I.—Climatic Data for Southeastern Coastal New England (from U.S.D.A. Yearbook, 1941)

Station	January avg.	July avg.	Maximum	Minimum
Nantucket, Mass.	32.6°F.	68.0°F.	92°F.	— 6°F.
Boston, Mass.	26.0	70.0	99	—21
Providence, R. I.	29.5	72.5	100	—17
New Bedford, Mass.	30.7	70.7	102	—12
New Haven, Conn.	29.7	72.6	101	—15

The maritime location of these islands is reflected in the temperature records of this region. (Table I) Although these data are inconclusive, they are representative and indicate that the offshore islands have a distinctly more equable climate than the adjacent mainland.

PRESENT VEGETATION

The distribution of vegetation types found on Martha's Vineyard is shown in Figure 1. The boundaries shown in the diagram have been drawn from aerial photographs and field observations, and are, of course, approximate. For convenience in mapping, some habitat types have been combined: (1) Beach, (2) Salt marsh-Brackish mud flats-Brackish ponds, (3) Fresh water ponds-Swamps-Bogs, (4) Grassland, (5) Scrub-Coppice Forest, (6) Woodland. The vegetation characteristic of these habitats will not be discussed here, but can be found in Ogden (1958).

Bicknell's (1919) flora of Nantucket lists 1108 species of vascular plants, of which 31 per cent are introduced. Of the remaining 69 per cent, over one-half were described as having southern affinities. Fewer than 20 per cent of the native plants were considered to represent northern types. In the Elizabeth Islands, Fogg (1930) described 558 native species and 128 introduced ones. Of the native species, approximately 20 per cent were southern types, and only 9 per cent showed northern affinities.

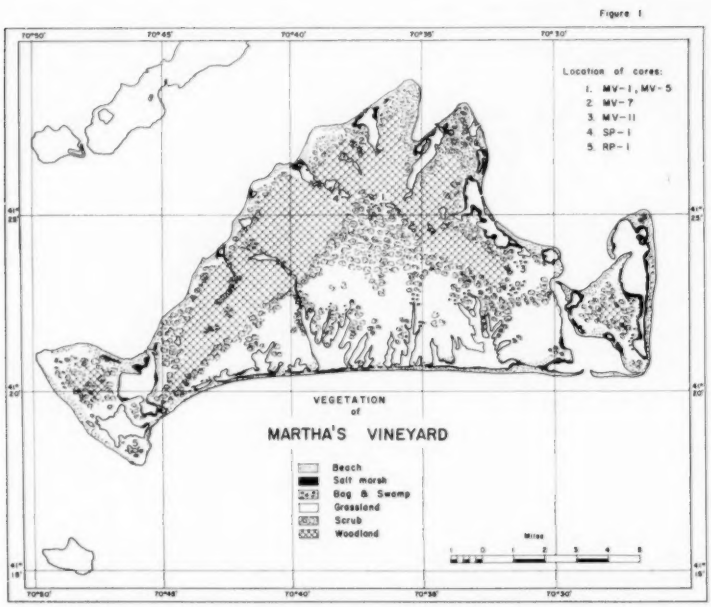


Fig. 1.—Distribution of major vegetational units on Martha's Vineyard. Boundaries determined from aerial photographs and field mapping. Core sites 1-5 indicate locations of samples shown in Figure 3.

Because of the lack of botanical information concerning Martha's Vineyard and the necessity of characterizing the pollen-producing environments there, a list of the plants noted by both Fogg and Bicknell was compiled. Collections and observations were also made in selected localities and added to the list. The number of species whose distribution is primarily south or north of Martha's Vineyard is summarized in Table II. Although no particular importance can be

TABLE II.—Summary of species with northern or southern affiliations

Habitat	No. spp.	No. northern	No. southern	% northern	% southern
Beach	18	6	3	33	17
Salt Marsh	29	6	7	21	24
Bogs, Ponds, Swamps	119	35	18	29	15
Grasslands	85	16	13	19	15
Scrub	60	13	18	22	30
Woodland	64	16	14	25	22

attached to the individual "habitat affiliation" figures (Distribution and range from Fernald, 1950), approximately 27 per cent of the species in this list have southern affiliations, and 33 per cent are primarily of more northern distribution. If this is a valid sample, it indicates that the earlier qualitative observations of Fogg and Bicknell were correct in considering the flora of the Vineyard to be more boreal than that of the other islands. There are far more than 273 species of vascular plants of Martha's Vineyard, but the plants included in this summary are characteristic and the dominant members of the communities in which they occur.

There are a few plants on Martha's Vineyard whose presence marks either a southern or northern limit of distribution. There are no records of new species from Martha's Vineyard, although Bicknell (1919) described a serviceberry, (*Amelanchier nantucketensis,* Bickn.) from Nantucket. This plant is also found on Martha's Vineyard.

MODERN WOODLANDS OF MARTHA'S VINEYARD

None of the woodlands of the Vineyard can be called forests. Some of the better woodlands will probably develop into stratified communities barring further disturbance. These "good woodlands" are restricted to the protected valleys and slopes of the moraine that forms the northwest coast of Martha's Vineyard. The most prominent trees in these stands are white oak, *Quercus alba;* beech, *Fagus grandifolia;* and sassafras, *Sassafras albidum.* These three constitute more than 60 per cent of the tree species on the better sites. Other trees in association with these are: black gum, *Nyssa sylvatica;* black oak, *Quercus velutina;* red oak, *Quercus borealis;* hop hornbeam, *Ostrya virginiana;* pignut hickory, *Carya glabra;* red maple, *Acer rubrum;* American holly, *Ilex opaca;* grey birch, *Betula populifolia;* white birch, *Betula papyrifera* (introduced); black cherry, *Prunus serotina;* dogwood, *Cornus florida;* and aspen, *Populus tremuloides.* Trees characteristic of old-field succession on the island include: pitch pine, *Pinus rigida;* red cedar, *Juniperus virginiana;* and black locust, *Robinia Pseudo-acacia.*

Common understory shrubs include: hobblebush, *Viburnum alnifolium;* highbush blueberry, *Vaccinium corymbosum* and *V. atrococcum;* witch hazel, *Hamamelis virginiana;* sweet gale, *Myrica gale;* bayberry, *M. pensylvanica;* serviceberry, *Amelanchier canadensis;* Nantucket serviceberry, *A. nantucketensis;* black alder, *Ilex verticillata;* sweet pepperbush, *Clethra alnifolia;* clammy azalea, *Rhododendron viscosum;* dog hobble, *Leucothoe racemosa;* male blueberry, *Lyonia ligustrina;* dangleberry, *Gaylussacia frondosa;* black huckleberry, *G. baccata;* and poison ivy, *Rhus radicans.*

There are a few large trees on the Vineyard and all of the original woodland was cut for firewood or lumber during the early colonial period of the island. Table III lists a few of the largest trees on the island today. This woodland, known as Priester's Woods, is the only area which has developed a definite understory. The greater part of

TABLE III.—Big trees of Priester's Woods, West Tisbury, Massachusetts

Name	DBH (in.)
Black Locust (*Robinia pseudo-acacia*)	17
Black Cherry (*Prunus serotina*)	18.5
White Oak (*Quercus alba*)	35
White Oak (*Quercus alba*) — (Multiple stem BH)	43.5
Beech (*Fagus grandifolia*)	49
Beech (*Fagus grandifolia*)	38
Red Maple (*Acer rubrum*)	32

the wooded area of Martha's Vineyard is covered with stands of pine (*Pinus rigida*), oak (*Quercus alba, Q. Borealis,* and *Q. velutina*), or mixed stands of pine and oak. The growth is characteristically scrubby and extensive tracts of multiple-stemmed oaks between 4 and 6 inches DBH indicate intensive and repeated burning. A few conspicuously older trees in these stands show healed fire scars.

SUCCESSION

The general course of plant succession on abandoned crop and pasture land of the Vineyard resembles the Juniper-Oak succession of the New Jersey Piedmont (Bard, 1952) more closely than the grey birch-oak phases described by Lutz (1928) and Raup (1940) for the granitic upland areas of New England. The first tree species to

Fig. 2.—Salt-blast shaping of woodland near shore. Note Juniper (*Juniperus virginiana*)—pitch pine (*Pinus rigida*) succession in foreground.

invade abandoned crop and pasture land on Martha's Vineyard is red cedar, *Juniperus virginiana* (Fig. 2). Unlike the New Jersey Piedmont, however, seedlings of pitch pine (*Pinus rigida*) begin to appear soon after cedars become established. In a few years, the pines form an almost pure stand, with a few seedlings of the oaks which eventually replace the pines. Black oak and red oak are usually more abundant than white oak during the early stages of pine replacement. The black and red oaks form a tangled, multi-stemmed growth within which the white oaks develop. The dense stands of black and red oak force the white oaks into a straight-stemmed habit. It is only after the large, older, black and red oaks begin to die out that more mesic trees, such as sassafras, pignut hickory, beech, and gum appear.

The time required to produce the "pro-forests" is difficult to determine. The pine stands, which form the earliest woodlands on abandoned fields, are usually between 50 and 100 years old when the oaks become prominent. Tree-ring counts of cut cedars indicate that the pines generally become established between 15 and 40 years after the fields are abandoned. In stands where saplings of hickory, beech, and sassafras are found among the predominantly straight-stemmed white oaks, tree-ring counts of the old stag-headed black and red oaks indicate that they are between 125 and 250 years old. Two white oak stumps in Priester's Woods yielded tree-ring counts of 285 and 330 years.

It is impossible to determine the age of the stands accurately by diameter classes. In a woodland not far from Priester's Woods, two black oaks were sampled with an increment borer. One, which had three main trunks averaging 6 inches in diameter was nearly the same age as a nearby single-stemmed tree that was 11.5 inches in diameter.

The Vineyard today, therefore, is somewhat bedraggled in a vegetational sense. The dependence of the early colonists on the forests for timber and fuel is evidenced by the depauperate woodlands. The following discussion deals with the somewhat meagre evidence that is available concerning the precolonial forest and its uses.

PRE-COLONIAL FORESTS OF MARTHA'S VINEYARD

The earliest record of the flora of Martha's Vineyard and the adjacent islands is contained in two journals from the voyages of Bartholomew Gosnold. The account written by Archer (1625) in the form of a diary, is primarily concerned with sailing directions and place descriptions. Brereton's (1602) journal records the plants, animals, and inhabitants of the islands. Although the "colonists" remained only three weeks, Gosnold is generally credited with having made the first settlement in New England which is supported by historical evidence. The exact location of the islands mentioned in the journals is a matter of some dispute. Banks (1911) believes that the first landfall among these islands was on the island that is now called

No Man's Land, although Brereton calls it "Marthaes Vineyard." Of this island, Brereton writes:

> The chiefest trees of this Island are Beeches and Cedars; the outward parts all overgrown with lowe bushie trees, three or four foot in height, which beareth some kinde of fruits, as appeared by their blossomes (Beach plums, *Prunus maritima?*); Strawberies, red and white, as sweet and much bigger than ours in England, Rasberies, Gooseberies, Hurtleberies, and such; an incredible store of Vines, as well in the woodie part of the Island, where they ran upon every tree, as on the outward parts, that we could not goe for treading upon them: . . .

Of the same island, Archer (1625) writes, ". . . the place is most pleasant . . . we went ashore and found it full of wood, vines, goosebery bushes, whortleberies (*Vaccinium macrocarpon?*), raspberies, and eglantines (*Rosa rugosa?*)." The Red Whortleberry, (*Vaccinium myrtillus*) of England and Scotland (Hendricks, 1919) does not occur in North America. The Large, or American Cranberry (*V. macrocarpon*) is very common on the offshore islands and resembles *V. myrtillus* sufficiently to be mistaken for it. The American Cranberry occurs on coarse sandy soils near the coast where tree growth is sparse, rather than in open bogs, swamps, and wet shores (Fernald, 1950). Although *Rosa rugosa*, the beach rose is described (Fernald, 1950) as being introduced and naturalized from Asia, there is no other native plant with which the colonists could have confused the well-known eglantine (Hendricks, 1919).

Anyone familiar with the shore regions of these islands will realize that this is an accurate description of what may be seen today on the coasts of most of these islands. Large numbers of beach plums (*Prunus maritima*), beach rose (*Rosa rugosa*), and cranberries (*Vaccinium macrocarpon*) are near the beach, and great quantities of wild grape (*Vitis Labrusca*) cover many of the trees and most of the ground adjacent to the beaches.

Although this island may have been Martha's Vineyard, there are some discrepancies in the chronicles which make this interpretation unlikely. Brereton speaks of an island "Foure English miles in compasse. . . ." Archer mentions that the island is "five miles in circuit." This part of the description fits No Man's Land very well. The chronicler (Brereton) goes on, however, to describe ". . . many springs of excellent sweet water, and a great standing lake of fresh water, neere the sea side, an English mile in compasse. . . ." This description does not resemble anything now found on No Man's Land. The description does fit the present island of Cuttyhunk, the most seaward of the Elizabeth Islands. Unfortunately, the next few paragraphs in Brereton's account make Cuttyhunk an impossibility, for he writes, ". . . from hence we went to another island, to the Northwest of this, and within a league or two of the maine, which we found to be greater than before we imagined, being 16 English miles at the least in compasse; . . ."

There are no islands to the northwest of Cuttyhunk, and of the islands to the northeast (the Elizabeth Islands, Naushon, Pasque, Nashawena), none are "16 English miles in compasse . . ." If the first island was No Man's Land, however, then this island would have to be the present Martha's Vineyard. A difficulty with this interpretation is the fact that the Vineyard is nearer to sixty miles in "compasse" than sixteen. Banks (1911) believes that the second island was the present Martha's Vineyard. Howe (1943) on the other hand, believes that the first island described by Brereton and Archer was Martha's Vineyard and was so named by them. Archer's account, however, makes it more probable that the first island was No Man's Land, for he writes, " . . . we set sail (from the first island), and doubled the cape of another island next unto it, which we called Dover Cliff . . . " These cliffs could only be the Gay Head cliffs of Martha's Vineyard. Both authors refer to the red and gray clays that can be found there.

If the ship's company actually did fortify an island in a lake on Cuttyhunk Island (as both Howe, 1943 and Banks, 1911 agree), then the concluding paragraph from Archer's account confirms the identification of the islands. Archer writes, " . . . we set sail, doubling the rocks of Elizabeth's Island (Cuttyhunk and Sow and Pigs Reef), and passing by Dover Cliff (Gay Head Cliff on Martha's Vineyard), came to anchor at Martha's Vineyard (No Man's Land) . . . (The following day) we set sail and bore for England . . . "

Both Banks (1911) and Howe (1943) point out that the place descriptions and locations could have been deliberately confounded to prevent rival navigators from finding the area and capitalizing on the published descriptions. If the "Dover Cliff" of Archer's account is the present Gay Head Cliff of Martha's Vineyard, the following quotation from Brereton refers to the vegetation of Martha's Vineyard (modern):

> This island (the second island) is full of high timbered Oaks, their leaves thrice so broad as ours; Cedars straight and tall; Beech, Elme, Hollie, Walnut trees in abundance, the fruit as bigge as ourse, as appeared by those we found under the trees, which had lien all the yeere ungathered; Hazlenut trees, Cherry trees, the leafe, barke, and bignesse not differing from ours in England, but the stalke beareth the blossomes or fruit at the end thereof like a cluster of Grapes, forty or fifty in a bunch; Sassafras trees great plentie all the Island over, a tree of high price and profit; also divers other fruit trees, some of them with strange barks, of an Orange colour, in feeling soft and smoothe like Velvet; in the thickest part of these woods, you may see a furlong or more round about. . . . Also, in every Island, and almost every part of every Island, are great store of Ground nuts, fortie together on a string, some of them as bigge as hennes egges; they grow not two inches under ground; the which nuts we found to be as good as Potatoes.

In a subsequent portion of the chronicle, Brereton also mentions

"Cypres trees, and Cotton Trees . . . ", which are probably *Populus* sp. and *Juniperus* sp., respectively. The "Cedars, tall and straight . . ." are probably the coast White cedar, *Chamaecyparis thyoides.* Extensive swamps containing large specimens of this tree are known from Cape Cod and other parts of New England (Deevey, 1948; Nichols, 1935). The walnut trees of the chronicle are undoubtedly hickories, as walnut was a general term for both walnut and hickory in early writings. The cherry trees can only be the Wild Black Cherry, *Prunus serotina,* which is one of the most common roadside trees on Martha's Vineyard today. The "fruit trees" with velvety-orange bark are much more difficult to recognize. A common open-field plant, which does attain the size of a small tree, is the staghorn sumac, *Rhus typhina.* The only other tree which comes to mind is the hophornbeam, *Carpinus caroliniana,* however, the bark is hardly velvety and the trunk a very dubious orange color.

On the basis of the description of the ground nuts by Brereton, " . . . in every Island, and almost every part of every Island . . . as bigge as hennes egges . . . " it seems likely that the groundnut, or wild bean, *Apios tuberosa* is indicated. Hendrick (1919) remarks that these groundnuts had a flavor not unlike potato.

Two comments from Brereton's chronicle give some clue to the structure of the forest, " . . . the woods of this island were full of high timbered Oaks . . . (and) in the thickest part of these woods, you may see a furlong or more round about . . . " In view of the detail with which Brereton recorded the trees which he saw, there is little reason to doubt that he did see "high timbered oaks . . . ", a situation not found in any part of the island of Martha's Vineyard or any of the other islands today. Because of dense underbrush and multi-stemmed growth of the modern woodlands, it is difficult to see 50 yards in the best of the woodlands, much less the 200 or more yards indicated in the journal. These two statements would seem to indicate that some parts, if not most of the island was covered with a high canopy forest, a condition not approximated by any of the modern woodlands of these islands.

Another indication of sizeable trees in the early Vineyard forests is the record of a whaling ship 135 feet long, of 65 tons burden, that was constructed of Vineyard timber prior to 1850 (J. C. Allen, personal communication). Although the keel was spliced, there are no oaks on the Vineyard today which approach the dimensions required for this construction. All of the native woodlands were eventually cut, and most of the cleared land was used for pasturing and farming (Banks, 1911). It is impossible to walk anywhere on the island today without seeing stone walls cris-crossing through the woods.

The colonists were not blind to the effects of clear-cutting and the potential denuding of the landscape. Many farmers maintained woodlots for household firewood, fence posts, and gate timbers. There is at least one well-authenticated instance in which two families cut

all of their stove and winter firewood from a 40 acre plot for well over 100 years (J. C. Allen, personal communication). Colonial axemen can be rated by the character of the stump sprout woodland which they left: a good axeman left a single "header" from which a single sprout would develop; a careless, or unskilled axeman would leave a "frazzled head" from which two or more sprouts would develop. This is evident in woodlands now found on croplands abandoned 75 or 100 years ago. Stem measurements and three-ring counts indicate that "single sprouts" may be twice the diameter of multiple sprout stems, even if they are of the same age.

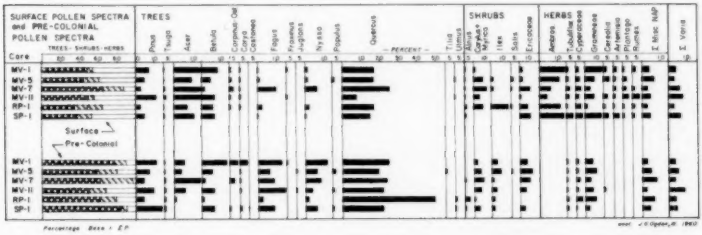


Fig. 3.—Pollen spectra from selected cores on Martha's Vineyard. The sample locations are shown in Figure 1. The upper six samples represent the modern vegetation in the vicinity of the sample site, and the lower six samples represent the pre-colonial vegetation (based on the lack of clearance/agriculture pollen indicators in the Herb columns on the right of the diagram). The sum of tree pollen is shown with double hatching in the block diagram at the left; the sum of herbaceous pollen is shown with single hatching; and the sum of herbaceous pollen (exclusive of the pollen of aquatic plants) is shown clear. The bar graphs represent the per cent of all pollen of each type at that level. A per cent scale is shown at the top of each histograph to facilitate comparison.

EVIDENCE FROM POLLEN ANALYSIS

A comparison of pollen spectra from surface samples of modern lakes and bogs on Martha's Vineyard with pollen spectra from pre-colonial times is shown in Fig. 3. The location of the sampling sites is shown in Fig. 1. The laboratory methods used to prepare the samples have been described elsewhere (Ogden, 1959). The principal criterion for the selection of the latest pre-colonial pollen sample was the absence of any European weed pollen (*Plantago, Rumex, Artemisia* cfr. *maritima*).

There is a higher representation of tree species in the pre-colonial samples than in the surface (modern) samples, due primarily to the abundance of Ambrosia type and Grass pollen in the surface samples (Fig. 3). The most significant results of this approach can be seen in a comparison of the trees contributing to the pollen samples in each of the two sample series. There is very little hemlock, hickory,

ash, walnut, cottonwood, basswood, or elm pollen in either of the sample series. There is no chestnut pollen in either sample series. Beeech and gum appear to exhibit a reciprocal relationship with the pollen of maple. Although species identification of maple from pollen alone is not very reliable, the pollen types identified, as well as the present distribution of maple of the Vineyard, indicates that these are probably the pollen grains of red maple (*Acer rubrum*). The decrease in beech and gum in the modern forests is apparently real, and reflects a former forest composition which contained many more specimens of these trees.

These data indicate that the pre-colonial forests of Martha's Vineyard did not contain any different trees than are now found on the island, but rather, that the present "better woodlands," now found only in restricted sites in a small part of the island, were once more widespread. Brereton's chronicle mentions, " . . . Walnut trees (Hickory) in abundance . . ." In the present Vineyard woodlands, hickory is not common, and is found only in the more mature woodlands within which a definite understory has developed. The cutting and burning practices of the early colonists could be expected to eliminate those tree species which could not readily form stump sprouts or those species which were especially prized for their wood. Species which can form stump sprouts readily, such as oak, could be expected to survive. Oak is also able to withstand the decrease in soil moisture that accompanies wholesale clearing better than the more mesic trees such as beech and gum.

Another factor influencing the process of revegetation after abandonment of fields on the Vineyard is salt-blast. Once the fields are open to the sweep and force of winter storms, the toxic effects of wind-blown salt (Boyce, 1954) undoubtedly limit reforestation, especially in the coastal areas (Fig. 2).

The picture of the colonial and pre-colonial forests which emerges from these observations is still incomplete. Nevertheless, the following generalizations seem justified on the basis of the evidence described in the preceding paragraphs:

1. The scrubby nature of the modern woodlands can be attributed to the formation of stump sprouts in areas cut over by colonial axemen. Destruction of seed sources and salt-blast have limited reforestation.

2. At least some portions, if not all, of the Vineyard were covered with a high canopied mature forest when the first colonists arrived.

3. Hickories were probably more abundant in the pre-colonial forests than at present.

4. Hemlock, chestnut, ash, walnut, basswood, and elm were either absent from or a very minor constituent of the pre-colonial forests.

REFERENCES

ARCHER, GABRIEL 1625. *Purchas his Pilgrims,* p. 121-141. *In* Mass. Hist. Soc. Coll. Ser. 3, Vol. 8. 1843.

BANKS, CHARLES E. 1911. The History of Martha's Vineyard, Massachusetts. Vol. I, General History, 535 p.; Vol. II, Town Records, 550 p. Dean Co., Boston, Mass.

BARD, GILY E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecol.* Monographs, **22**:195-215.

BICKNELL, EUGENE P. 1908-1919. The ferns and flowering plants of Nantucket. *Bull. Torrey Bot. Club,* vols. 35-46.

BOYCE, S. G. 1954. The salt-spray community. *Ecol.* Monographs, **24**:29-67.

BRERETON, J. 1602. A Briefe and true Relation of the Discoverie of the North part of Virginia & c. Geor. Bishop, London. 24 p.

BROMLEY, S. W. 1935. The original forest types of southeastern New England. *Ecol.* Monographs, **5**:61-89.

DEEVEY, E. S., JR. 1948. On the date of the last rise of sea-level in southern New England, with remarks on the Grassy Island site. *Am. J. Sci.,* **246**:717-752.

FERNALD, M. L. 1911. A botanical expedition to Newfoundland and southern Laborador. *Rhodora,* **13**:109-162.

———. 1950. Grays Manual of Botany, 8th ed. American Book Co., New York, 1632 p.

FISHER, R. T. 1933. New England Forests: Biological Factors, p. 213-223. *In* New England's Prospect, 1933. Amer. Geog. Soc., Spec. Publ. **16**.

FLINT, R. F. 1957. Glacial Geology and the Pleistocene Epoch. 2d ed. John Wiley and Sons, New York. 353 p.

FOGG, J. M. 1930. Flora of the Elizabeth Islands, Massachusetts. *Rhodora,* **32**:119-281.

HEDRICK, U. P. 1919. Sturtevant's Notes on Edible Plants. New York Agr. Expt. Sta. 27th Ann. Report, Vol. 2, Part II. 686 p.

HOLLICK, A. 1894. Observations on the geology and botany of Martha's Vineyard, Massachusetts. *Trans. N. Y. Acad. Sci.,* **13**:8-22.

HOWE, H. F. 1943. Prologue to New England. Faraar and Rinehart, New York. 324 p.

LUTZ, H. J. 1928. Trends and silvicultural significance of upland forest succession in southern New England. Yale Univ. School of Forestry. Bull. 22. 18 p.

NICHOLS, G. E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. *Ecology,* **16**(3):403-422.

OGDEN, J. G. III., 1958. Wisconsin Vegetation and Climate on Martha's Vineyard, Massachusetts. Unpubl. PhD. thesis, Yale University, New Haven, Conn.

———. 1959. A late-glacial pollen sequence from Martha's Vineyard, Massachusetts. *Am. J. Sci.,* **257**:366-381.

RAUP, H. M. 1937. Recent changes in climate and vegetation in southern New England and adjacent New York. *J. Arnold Arboretum*, **18**:79-117.

———, 1940. Old field forests of southern New England. *Ibid.*, **21**:266-273.

SEARS, PAUL B. 1932. Postglacial climate in eastern North America. *Ecology*, **13**:1-6.

SHALER, N. S. 1886. Geology of Martha's Vineyard. *U. S. Geol. Survey Ann. Report*, **7**:303-361.

U. S. DEPT. OF AGRICULTURE YEARBOOK 1941. Climate and Man. Washington, D. C. 1648 p.

WOODWORTH, J. B., AND E. WIGGLESWORTH 1934. Geography and Geology of the Region including Cape Cod, the Elizabeth Island, Nantucket, Martha's Vineyard, No Man's Land, and Block Island. Mus. Comp. Zool. Harvard, Memoir 52. 338 p.

The Red Eye Pigment Content of the Drosophila affinis Subgroup Species

B. W. GEER[1]

Department of Genetics, University of California, Davis

ABSTRACT: The red eye pigments of *Drosophila algonquin*, D. *azteca*, *D. melanogaster*, *D. narragansett*, *D. pseudoobscura*, and *D. tolteca* were analyzed. The determinations confirm the close relationship of the *D. obscura* group species as compared to *D. melanogaster*. *D. azteca* and *D. tolteca* appear to be very closely related; whereas, *D. pseudoobscura* was shown to possess an appreciably lower amount of red eye pigment than the *D. affinis* subgroup species.

A definite correlation was found to exist between the size of the eye and the red pigment contained therein, but the relationship varied from species to species. Instances of significantly great variability between strains of single species were found in *D. affinis* and *D. melanogaster*.

The fact that the color of the eye of wild-type *Drosophila* is due to two pigments, red and brown, resulting from two different biosynthetic pathways has been established by several experimental techniques. The identification of the sequence involved in red pigment formation has been particularly difficult to elucidate and only in recent years has the mystery begun to be unveiled. A number of pteridines which are ostensive precursors of red pigment have been identified (Hadorn and Mitchell, 1951; Forrest and Mitchell, 1954, 1955; Forrest, Hatfield, and Van Baalen, 1959). Visconti, Hadorn, and Karrer (1957) isolated three red pigments from the eye of *Drosophila melanogaster* by paper chromatography. These pigments, apparently closely related to their pteridine precursors, have been named drosopterin, isodrosopterin, and neodrosopterin, and they may be extracted simultaneously and measured quantitatively.

Members of the *D. affinis* subgroup are widely distributed geographically (Miller, 1958) and are very similar and closely related as evidenced by the mating experiments of Ensign (1960), Miller (1950a, 1950b), and Ensign and Miller (1957). Sulerud (1958) has indicated that the sex combs and tarsi of these species may be promising criteria for identification purposes and that overlapping of characteristics does occur although it is limited.

The purpose of this study is to determine whether the red pigment content of the *D. affinis* subgroup might be used as an aid in establishing the relationships of the individual members which are considered.

---

[1] This paper is taken from a master's thesis presented to the University of Nebraska and is contribution number 333 of the Zoology Department of the University of Nebraska.

Acknowledgments.—I am deeply indebted to Dr. Dwight D. Miller who served as my advisor during the tenure of this research and who supplied many stimulating comments and suggestions. Gratitude is also extended to the Zoology and Physiology Departments of the University of Nebraska who made their research facilities available to the author.

EXPERIMENTAL METHODS

Species and strains of *Drosophila* used for the major portion of this study were: *D. affinis,* Missouri (Halls) and North Carolina (Raleigh); *D. algonquin,* Nebraska (Humboldt) and Minnesota (Halstad); *D. azteca,* Mexico (Durango) and California (Mather); *D. melanogaster,* Nebraska (Niobrara State Park) and Texas (Waxahachie); *D. narragansett,* New York (Lebanon); *D. pseudoobscura,* British Columbia (Kelowna) and Mexico (Hidalgo); and *D. tolteca,* Mexico (Chapuluacán) and Bolivia (Coroicó).

The inclusion of the strains of *D. melanogaster* and *D. pseudoobscura* was stimulated by the earlier work of Nolte (1958) in which he demonstrated a decisive difference between the pigment contents of the eyes of these two species. All the strains utilized were established from a single wild female except the Minnesota strain of *D. algonquin* which is a mixed strain. Because it was thought that any intraspecific variations might be revealed by using strains established from flies far removed from each other, each species, except for *D. narragansett,* was represented by widely separated strains from two localities.

Ephrussi and Herold (1944) showed that the amount of red pigment decreases with an increase in temperature. The total amount of pigment is also dependent on the size of the eye and thus presumably is related to the size of the fly. Thus it was desirable to acquire flies of optimum adult size for experimental analysis; consequently, the flies were grown on freshly prepared cornmeal medium which was supplemented with an abundance of live yeast and the temperature was controlled at 18 $\pm$ 2° C. To avoid overcrowding of the larvae and adult flies, eggs were collected and the number of flies per bottle of culture medium was limited to less than 120.

In regard to the adult flies, Ephrussi and Herold (1944) have shown that there is a change in red pigment content of the eye with increase in age; however, the increase of pigmentation does reach a point of stability after several days. The period of time before the red pigment content became stable was found to be slightly longer than the five-day period that Ephrussi and Herold indicated; consequently, the adult flies were aged for a ten-day period after which no increase in red pigment deposition was evident.

The extraction procedure utilized was essentially that of Ephrussi and Herold (1944). The solvent which has been named AEA was prepared by adding 1.0 ml of concentrated HCl to 1000 ml of 30% ethyl alcohol. A large volume of AEA was made up and used throughout the experimental work. The pH of the solvent was checked period-

ically with a Macbeth Continuous Operating pH Meter, and it was found that the pH did not deviate from 2.0 during the time that the AEA was being used; therefore, the solvent was not a variable.

The heads of the flies were removed and diameter of the head was recorded by measuring across the eyes with a 2 mm micrometer. The heads were then partially split between the eyes with the edge of a razor blade and extracted in the dark at 18 ± 2° C with AEA for 2½ to 3 days. The size of each sample was 20 heads per 4.0 ml of AEA.

Following extraction the light absorption of the solution containing the red pigment was determined photometrically through the 400-540 mμ light spectrum with a Beckman D. U. Spectrophotometer and 485 mμ was found to be the maximum. The results of the light absorption measurements of the red pigment extracts will be given in terms of extinction, log I_0/I.

The red pigment solution behaves as a redox system, being light brown in the oxidized state and colorless in the reduced state. However, Ephrussi and Herold have clearly shown that the extracted pigment is in the state of maximum oxidation; therefore, no precaution was necessary to control the oxidation state of the extracts.

RESULTS AND DISCUSSION

Following the methods outlined, flies were raised under controlled conditions in an attempt to obtain adult flies of optimum and uniform size. By measuring the diameter of the decapitated heads the uniformity of head size was under close observation, and it was readily observed that there was a striking variation of head size between species (Tabes I and II). This was true although all species are members of the *D. obscura* group except *D. melanogaster;* and, moreover, *D. affinis, D. algonquin, D. azteca, D. narragansett,* and *D. tolteca* are members of the *D. affinis* subgroup. *D. algonquin* and *D. pseudoobscura* were found to have comparatively large heads; whereas, *D. tolteca* and *D. azteca* had small heads, and the other species were intermediate in size.

The diameter of heads of females was found to be greater than that of males, and this was also true of body structure in general. The means of head diameter of each sex of the laboratory strains are given in Tables I and II, are accompanied by the standard error and range of individual samples to facilitate visualization of the variability.

Variability was found to be relatively large between individual flies. This might be explained by differences in larvae feeding conditions; however, the adult flies emerged from pupae within a two day span. Therefore, differences in feeding conditions with which the larvae were confronted should have been slight. In spite of the individual variance, the means of the head diameters of the samples within a strain were found to exhibit less variability, and in most instances the variability was less than 3%

Qualitatively the red eye pigment extract was the same for all the laboratory strains that were tested. The curve formed by plotting extinction against light wavelength was similar to that which has been described by Nolte (1952) and others. The rather broad peak which is formed in this manner is the result of the mixture of at least three different drosopterins with slightly varied absorption maxima. The values given in Tables I and II are the extinction values at 485 mμ for the extract of twenty heads in 4 ml of AEA.

In regard to the red eye pigment content of the laboratory strains that were tested, a similar variance was found to exist in comparison

TABLE I.—The means for head diameter in mm and extinction of the red pigment extract are given for the males of the laboratory strains that were tested; the number of samples (n) is indicated

Laboratory strains	n	Head diameter	Extinction at 485 mμ
D. affinis			
Missouri	4	0.817±0.005	0.471±0.008
		(0.805—0.827)	(0.453—0.491)
North Carolina	4	0.806±0.007	0.381±0.009
		(0.793—0.820)	(0.364—0.403)
D. algonquin			
Nebraska	4	0.883±0.004	0.452±0.005
		(0.876—0.895)	(0.438—0.463)
Minnesota	4	0.847±0.002	0.440±0.005
		(0.842—0.851)	(0.427—0.448)
D. azteca			
Mexico	4	0.776±0.003	0.337±0.005
		(0.768—0.784)	(0.327—0.349)
California	4	0.800±0.004	0.346±0.006
		(0.795—0.812)	(0.331—0.356)
D. melanogaster			
Nebraska	4	0.786±0.006	0.438±0.016
		(0.781—0.800)	(0.401—0.456)
Texas	4	0.776±0.003	0.489±0.007
		(0.770—0.782)	(0.476—0.502)
D. narragansett			
New York	4	0.782±0.005	0.438±0.010
		(0.768—0.792)	(0.421—0.455)
D. pseudoobscura			
British Columbia	4	0.892±0.007	0.399±0.003
		(0.885—0.899)	(0.394—0.404)
Mexico	4	0.870±0.003	0.371±0.004
		(0.863—0.876)	(0.368—0.374)
D. tolteca			
Mexico	4	0.753±0.007	0.371±0.017
		(0.736—0.771)	(0.352—0.386)
Bolivia	4	0.742±0.008	0.350±0.007
		(0.728—0.761)	(0.338—0.365)

to the head diameter measurements. The females definitely exhibited greater amounts of red pigment than did the males; therefore, this would indicate that the pigment content was dependent upon the head diameter within a given strain of flies since females also had greater head diameters.

The foregoing results indicate a relationship between the head diameter and the total red pigment content of the eye. The pigment content variable was examined for its dependence upon the independent head diameter by utilizing a t-test. The regression coefficients for strains are given in Table III along with their t-values, and the

TABLE II.—The means for head diameter in mm and extinction of the red pigment extract are given for the females of the laboratory strains that were tested; the number of samples (n) is indicated

Laboratory strains	n	Head Diameter	Extinction at 485 mμ
D. affinis			
Missouri	4	0.883±0.006 (0.872—0.898)	0.564±0.003 (0.556—0.569)
North Carolina	4	0.869±0.004 (0.857—0.878)	0.470±0.011 (0.451—0.492)
D. algonquin			
Nebraska	4	0.956±0.002 (0.952—0.959)	0.527±0.003 (0.523—0.534)
Minnesota		0.931±0.004 (0.924—0.941)	0.511±0.010 (0.493—0.534)
D. azteca			
Mexico	4	0.833±0.004 (0.825—0.845)	0.382±0.006 (0.372—0.397)
California	4	0.854±0.006 (0.838—0.863)	0.387±0.006 (0.377—0.402)
D. melanogaster			
Nebraska	4	0.840±0.002 (0.837—0.846)	0.539±0.009 (0.522—0.561)
Texas	4	0.839±0.004 (0.833—0.847)	0.565±0.009 (0.542—0.582)
D. narragansett			
New York	4	0.853±0.002 (0.848—0.857)	0.515±0.004 (0.508—0.525)
D. pseudoobscura			
British Columbia	4	0.936±0.008 (0.920—0.951)	0.438±0.006 (0.427—0.448)
Mexico	4	0.918±0.004 (0.911—0.928)	0.416±0.004 (0.405—0.422)
D. tolteca			
Mexico	4	0.826±0.007 (0.804—0.836)	0.479±0.014 (0.443—0.506)
Bolivia	4	0.814±0.007 (0.786—0.837)	0.426±0.013 (0.392—0.454)

significance of the t-values is indicated. All t-values are significant at the 1% level. Undoubtedly the relationship was not the same for each of the strains that was tested or, consequently, the strains with the largest head diameter would also have been those with the greatest pigment content and vice versa. This point was put to test by applying analysis of covariance to see if the regression lines of the different strains might perhaps be parallel. This was found not to be the case; therefore, any adjustment of red pigment content values would be somewhat superficial and might tend to exaggerate the differences that occur.

TABLE III.—The regression coefficient, b, of the red eye pigment variable on the head diameter variable is given for each laboratory strain in addition to the correlation coefficient, r; the significance of b is indicated by t-values; all of which are significant at the 1% level

Laboratory strains	r	b	t
D. affinis			
Missouri	0.967	1.34	9.57
North Carolina	0.975	1.41	10.85
D. algonquin			
Nebraska	0.980	1.03	13.21
Minnesota	0.953	0.86	7.75
D. azteca			
Mexico	0.896	0.75	4.17
California	0.941	0.76	6.91
D. melanogaster			
Nebraska	0.970	1.86	16.20
Texas	0.886	1.11	4.63
D. narragansett			
New York	0.895	0.83	4.88
D. pseudoobscura			
British Columbia	0.855	0.71	3.94
Mexico	0.723	0.51	3.64
D. tolteca			
Mexico	0.989	1.48	16.44
Bolivia	0.968	1.02	9.27

Upon making intraspecific comparisons of red eye pigment content, one finds what appears to be striking differences between the Misssouri and North Carolina strains of *D. affinis* and the Nebraska and Texas strains of *D. melanogaster*. The differences within *D. algonquin, D. azteca, D. pseudoobscura,* and *D. tolteca* appear to be slight, and dissimilarities in size may account for any differences which might be present in the latter group; however, the diversity of the strains of *D. affinis* and *D. melanogaster* cannot be explained on this basis. *D. affinis* and *D. melanogaster* in this instance could be used to support the theory of polygenes which affect *Drosophila* eye pigmentation as proposed by Nolte (1959).

A comparison of species reveals that all species of the *D. obscura* group tested possess less red eye pigment than *D. melanogaster,* and that the values are more or less closely grouped. Patterson and Mainland (1944) are of the opinion that *D. tolteca* is more closely related to *D. azteca* than to any of the other members of the *D. affinis* subgroup, and this is borne out by examination of the data of head size and pigment content. Any other conclusions of this sort are purely speculative although there is some indication of a similarity of *D. affinis* and *D. narragansett;* however, the diversity exhibited by the two strains of *D. affinis* and the fact that only one strain of *D. narragansett* was tested make this a weak point. *D. algonquin* is the largest member of the *D. affinis* subgroup but it possesses no more red pigment than *D. affinis* or *D. narragansett* but has more red pigment than the less related *D. pseudoobscura,* although *D. pseudoobscura* individuals are much the same size.

Geographical distribution was not revealed to play any great role in pigment content differences in this investigation. There was a slight indication that northern strains tended to have greater head diameters at the temperature at which the flies were raised (18 C). It is possible that the genetic constitution of the northern strains favored growth at the relatively low temperature at which this investigation was conducted.

It is a reasonable assumption that the red eye pigments are by-products of metabolism and are at least in part dependent upon the rates of metabolism. Several observations make any general statement of the relationship impossible. As mentioned earlier in the paper Ephrussi and Herold (1944) demonstrated that the eye pigment content of wild-type *D. melanogaster* increases when the culturing temperature is reduced. Likewise, the rate of development of the flies is also decreased. Moreover, Ephrussi and Herold (1945) showed that the pigment content of the *D. melanogaster* mutant, blood, exhibited an increased pigment concentration at lowered temperatures. Nevertheless, in a limited number of observations by the author the mutant, honey, which is one of the pseudoalleles of the white locus as is blood, possessed less eye pigment at 16° C than at 25° C. This does not refute the work on blood but does indicate that the block in pigment synthesis of the two mutants may be affected differently by changes in the environmental temperature. Rasmuson, Green, and Ewertson (1960) have indicated that the block in pigment synthesis at the apricot locus is probably at an early step and it is likely that the influence of the blood and honey mutants are not far removed.

Considering the wild-type strains dealt with in this paper, the metabolic rate of *D. melanogaster* is greater as evidenced by its shorter developmental period which was 14 days as compared to 17-18 days for the members of the *D. obscura* group. Consequently, it cannot be stated that a reduction in the rate of the developmental processes stimulates a higher rate of pigment deposit or the members of the

D. obscura group would outrank *melanogaster* in red eye pigment content due to their longer developmental period. Hubby and Throckmorton (1960) have courageously attacked this problem from an evolutionary aspect, but in addition much more research is needed at the genetic level.

REFERENCES

ENSIGN, S. D. 1960. Reproductive isolation between *Drosophila tolteca* and related species. *Evolution*, **14**:378-386.

——— AND D. D. MILLER 1957. Sexual isolation in the *affinis* subgroup. *Drosophila Information Service*, **31**:117.

EPHRUSSI, B. AND J. L. HEROLD 1944. Studies of eye pigments of *Drosophila*. I. Methods of extraction and quantitative estimation of the pigment components. *Genetics*, **29**:148-175.

——— AND ——— 1945. Studies of eye pigments of *Drosophila*. II. Effect of temperature on the red and brown pigments in the mutant blood. *Ibid.*, **30**:62-70.

FORREST, H. S. AND H. K. MITCHELL 1954. Pteridines from *Drosophila*. *J. Am. Chem. Soc.*, **76**:5656-5662.

——— AND ——— 1955. Isolation of three more pteridines. *Ibid.*, **77**: 4865-4869.

———, D. HATFIELD AND C. VAN BAALEN 1959. Characterization of a second yellow compound from *Drosophila melanogaster*. *Nature*, **183**:1269-1270.

HADORN, E. AND H. K. MITCHELL 1951. Properties of mutants of *Drosophila melanogaster* and changes during development as revealed by paper chromatography. *Proc. Nat. Acad. Sci.*, **37**:650-655.

HUBBY, J. AND L. THROCKMORTON 1960. Evolution and pteridine metabolism in the genus *Drosophila*. *Ibid.*, **46**:65-78.

MILLER, D. D. 1950a. Observations on two cases of interspecific hybridizations with *Drosophila athabasca*. *Am. Nat.*, **84**:81-93.

———1950b. Mating behavior in *Drosophila affinis* and *Drosophila algonquin*. *Evolution*, **4**:123-124.

———1958. Geographical distribution of the American *Drosophila affinis* subgroup species. *Am. Midl. Nat.*, **60**:52-70.

NOLTE, D. J. 1952. The eye pigmentary system of *Drosophila:* the action of eye-colour genes. *J. Genetics*, **51**:143-186.

———1958. Eye pigment relationships in three species groups of *Drosophila*. *Evolution*, **12**:512-519.

———1959. Polygenes in eye pigment production in *Drosophila* species. *Ibid.*, **13**:1-9.

PATTERSON, J. T. AND H. B. MAINLAND 1944. The Drosophilidae of Mexico. *University of Texas Publication*, **4445**:9-101.

RASMUSON, B., M. M. GREEN AND G. EWERTSON 1960. Qualitative and quantitative analyses of eye pigments and pteridines in back-mutations of the mutant w^a in *Drosophila melanogaster*. *Hereditas*, **46**:635-650.

SULERUD, R. L. 1959. An investigation of possible aids for separating of the *D. affinis* subgroup species. *Drosophila Information Service*, **33**:165-166.

VISCONTI, M., E. HADORN AND P. KARRER 1957. Fluoreszierende Stoffe aus *Drosophila melanogaster:* die roten Augenfarbstoffe. *Helvetica Chimica Acta*, **40**:579-585.

Laboratory Life History of the Eastern Harvest Mouse[1]

STEPHEN V. KAYE

Health Physics Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee[2]

ABSTRACT: The gestation period of *Reithrodontomys h. humulis* appears to be approximately 21 days. The sizes of nine litters born in the laboratory ranged from two to four, with a mean of 3.2. A mean of 1.2 grams was recorded from the weights of 27 young at birth. The reproductive efficiencies of two females were 50.4 and 50.8 per cent, close to the highest known reproductive efficiency of any mammal.

Harvest mice at birth appear unpigmented, are pink, have a translucent skin, and have tiny, white natal hairs present on most parts of the body. By the end of the first week, the brownish hair on the head and nape almost completely hides the underlying skin. All young are weaned by the end of the third week and are cared for only by the female parent. Parent mice occasionally killed and ate their young, and on one occasion two 30-day-old females were killed and eaten by their two litter mates. Males get along well with females, although males rarely tolerate each other in the same cage. Females are exceedingly tolerant of members of their own sex.

The Eastern harvest mouse, *Reithrodontomys humulis humulis* (Audubon and Bachman), is one of the world's smallest rodents. It is distributed throughout the grasslands and old fields of much of the Southeast; and, although it occupies this extensive range, nowhere has it been found to be locally abundant (Hall and Kelson, 1959). A detailed study on the life history of the Eastern harvest mouse was nonexistent until Layne (1959) published an account of growth and development. Wherever possible, the results of the present study are compared with those reported by Layne (1959).

Audubon and Bachman (*circa* 1854) were the first to give an account of behavior and reproduction of the Eastern harvest mouse in captivity and to describe the type of habitat and ecologic relationships in which these mice were to be found. A captive female, on two occasions, gave birth to young; the first litter consisted of four young, the second of three. Brimley (1923), in a list of breeding dates of mammals found at Raleigh, North Carolina, comments that harvest mice bear from two to five in a litter and live in nests. The first account of daily growth and development of *Reithrodontomys h. humulis* was by Holding and Royal (1952). Developmental changes,

[1] The work reported here constituted part of the requirements for the M.S. degree in Animal Ecology at N. C. State College, Raleigh. I express my sincere gratitude to Dr. Frederick S. Barkalow, Jr., chairman of my graduate committee, for his helpful advice and direction.

[2] Operated by Union Carbide Corporation for the U.S. Atomic Energy Commission.

behavior, and measurements were recorded for a single survivor of a laboratory-born litter of two.

In this study a laboratory colony of Eastern harvest mice was maintained to study growth and development of young by recording daily weights, measurements, and developmental changes. Also, observations were made of feeding habits, food acceptance, care of young, and other behavior. All mice other than those born in the laboratory were live-trapped from fields at Raleigh, N.C.

MATERIALS AND METHODS

Care of mice.—A laboratory colony of *Reithrodontomys h. humulis* was maintained in cages from March 1958 to April 1959. Usually the colony consisted of 12 to 15 adult mice and one or two litters of young. Although the total number of individuals did not vary appreciably during the period of the investigation, the individual composition often changed due to mortality, escapes, sacrifice of animals, and addition of fresh stocks from the field.

The cages, constructed of ¾-inch wood and faced on one side with ¼-inch mesh hardware cloth, measured 29 by 13 inches in depth, and 16¼ inches in height. A nest box was attached to one of the outside walls of each cage. An opening 1½ inches in diameter joined the cage with the nest box 11 inches above the floor of the cage, but easy access to the nest box was provided through use of a 2-inch wide ramp of hardware cloth extending from the cage floor to the nest box. The nest boxes measured 10½ by 8½ inches in depth, and 7¾ inches in height. The top of the nest box was hinged to permit removal of the animals from the nest. The floor was concave, forming a depression in the center in which the harvest mice built nests from cotton provided for that purpose.

Weighing and measuring young.—Mice were weighed on a trip balance and measured with a steel rule during the first day after parturition and daily, at the same hour, until 20 days of age. After reaching this age, they were weighed and measured at intervals varying from two to five days until they were 50 days old. The following body measurements were taken: total length, tail length, left hind foot length, and ear length from crown to tip. The total length measurement was taken with the mice resting with the ventral side down rather than in the currently accepted ventral side up position. It was found that the baby mice struggled less and more accurate measurements could be obtained when they were measured in the belly down position. The usual ear notch measurements could not be obtained until the external auditory meatus opened at approximately 10 days of age. It was necessary, therefore, to start with measurements from cranium to ear tip in order to follow growth of this appendage from birth.

Young animals up to 12 days of age could be handled and measured easily, but older more active animals had to be anesthetized

with ether. The amount of ether used was sufficient to render the animal unconscious for about one minute. On two occasions too much ether was used and the mice died.

RESULTS

MATING BEHAVIOR

Mating attempts by captive male harvest mice were observed three times. In the first instance, the male chased the female for about one hour between the nest box and cage. During the entire time the female emitted high-pitched squeals. Several times the male tried to mount the female, but her repulsive action did not permit copulation.

Attempted mating was observed after a female harvest mouse was placed in a cage occupied by a male. The female went into the nest box where she was met by the male, the two touched noses, then cautiously sniffed each other. An attempt by the male to mount the female frightened her to such an extent that she stiffened and did not move. Soon the male gave up his advances and copulation did not occur.

Mating behavior was noted the day after a male and female were placed together in a cage. On this occasion the male chased the female for five minutes, nipping and biting at her tail and hind legs. The female thwarted his mating advances each time an attempt was made.

Evidently none of the described mating attempts was successful, because no young were born to the females after sufficient isolation time. The behavior of the three females indicates that they probably were not in estrus at the time of the observed attempted matings.

GESTATION PERIOD

Layne (1959) reports a 24-day minimum time between successive litters for *R. humulis;* in the present study, postpartum mating was not recorded. Two estimations of the gestation period were obtained.

On May 20, 1958, a female, isolated from other males for several weeks, was placed in a cage with a single male. Twenty-nine days later, this female bore a litter of two. Gestation in this case could have been a maximum of 29 days.

A more precise estimate was obtained when a male was placed in a cage with a female for a two-day period and then removed. Twenty-one days after the male was removed, this female gave birth to a litter of three. Since pregnancy could have occurred on either night the two mice were together, gestation was a minimum of 21 or a maximum of 22 days.

WEIGHTS, LITTER SIZES, AND SEX RATIOS AT BIRTH

The sizes of nine litters born in the laboratory to different mothers ranged from two to four, with a mean of 3.2 (Table I). Layne (1959) reported litter sizes of *R. humulis* to range from one to three, with a mean of 2.2 based upon nine litters.

The average weight of 27 young at birth was 1.2 g which agrees exactly with the mean weight of young reported by Layne. The mean weights of males and females treated separately in the present study did not differ from the mean weight of the sexes combined.

Eight of 11 litters mentioned in Layne's study were born to the same female. This female weighed from 6.5 to 7.0 g (nonpregnant

TABLE I.—Litter sizes, sex ratios, and weights of nine laboratory-born litters of Eastern harvest mice

Litter number	Size	No. ♂♂	No. ♀♀	Mean weight of young (grams)	Litter weight (grams)	Reproductive efficiency (per cent)
1	3	1	2	1.3	3.9	....
2	3	1	2	0.8	2.4	....
3	4[a]	1	1	1.2	4.7	50.5
4	2	1	1	1.3	2.6	....
5	3	3	0	1.2	3.6	30.8
6	4	0	4	1.3	5.3	43.1
7	3	1	2	..[b]	..[b]	....
8	4	1	3	1.4	5.7	50.4
9	3	0	3	1.2	3.6	....
Totals	29	9	18			
Means	3.2			1.2	4.0	43.7

[a] Sex not determined for two young of this litter.
[b] No weights taken at birth.

weight), or about 2.5 g lighter than the weights of the females in the present study. Since reproductive ability varies from female to female, it is possible that the female which produced the eight litters in Layne's study was one capable of having many litters but only a few young per litter. This situation might account for the difference between the average litter size reported here and that reported by Layne. The nine litters of harvest mice from which the data for the present study were obtained were all born to different females. It is apparent that the data of growth and development presented by Layne (1959) should be treated with caution because of the lack of an adequate number in the parental stock.

On four occasions the weight of the mother was taken immediately after the young were born, along with the weight of the litter. The weight of the litter multiplied by 100 and divided by the weight of the mother gives a factor called "reproductive efficiency." Reproductive efficiency is a useful measurement for interspecies and intraspecies comparisons. Reproductive efficiencies of 30.8, 43.1, 50.4, and 50.5 per cent were calculated for four individual females. The smallest figure is based upon a litter of three young, whereas the three larger efficiency figures are based upon litters of four young. Most mammals have a reproductive efficiency of 33 per cent or less with the highest

reproductive efficiency of any mammal on record being 53.2 per cent for *Microtus arvalis* (Frank, 1957).

Sex was determined for 27 animals born in the laboratory. Table I shows an unbalanced sex ratio, *i.e.*, 18 females to 9 males. Layne (1959) reported a sex ratio that was even at birth.

PARENTAL CARE OF YOUNG

The care of young is left entirely to the female which, a few days prior to parturition, drives the male from the nest box. The male would usually remain in a corner of the cage until provided with some cotton to build a nest. Sometimes the male himself took cotton from the nest previously shared with the female. During the few days preceding parturition and for a period of about three weeks thereafter, the male remained in his own nest and was not admitted to the nest box. One female allowed her mate to occupy the nest box, but not the same nest that contained the young. The male built a smaller nest a few inches from the maternal nest. After the young started eating solid food, the male would be admitted into the female's nest. One male in Layne's (1959) study occasionally joined his mate in defending the young. Whenever an attempt was made to remove young from a nest to be weighed and measured, their mothers always exhibited defensive behavior. A female would usually scoop the young under her body and commence to bite and push away any object used to obtain the young.

Several of the females would climb up the hardware cloth side of the cage and watch nervously while their young were being handled outside the cage; on the other hand, some mothers would remain quietly in the nest and repair the damage done in extracting the young. Maternal concern for the young diminished soon after the young started eating solid food.

As each baby mouse was returned to the nest, the mother would scoop it close to herself and wash it while manipulating it with her forepaws. The young would try to nurse while they were being washed, but the mother would not permit this until the preening was completed.

If a young mouse was placed a short distance from a nest, the mother would carry it into the nest, grasping the animal at any convenient place on its body with her jaws. The young were sometimes carried by one foot.

The inguinal pair and the two pairs of abdominal teats were the ones usually used for nursing. Only one litter, a litter of four, was known to nurse from the pectoral teats.

Because the mothers exhibited such protective concern for their young, it is hard to understand why they killed and ate so many of them. No less than nine individuals were killed and partially or entirely eaten by one or both parents. One mother killed and partially ate a young mouse that was 31 days old, and another female killed and ate two of her young that were one week old. These two females

had no mates in their cages. The killing and eating of six other young cannot be attributed solely to the female, because the mate was also present. Two 30-day-old females were killed and eaten by their two litter mates. There were no other mice in the cage at the time.

There is no doubt that the mice which were killed and eaten by their parents or litter mates did not first die of natural causes, because all were healthy at least one day before they were found consumed. Sometimes the only trace of a young animal was a tooth or a tuft of hair mixed with the nesting material. Svihla (1931) and Layne (1959) also commented on cannibalism in *Reithrodontomys*.

DEVELOPMENT OF YOUNG EASTERN HARVEST MICE

Eyes.—At birth, the eyes are covered by a semitransparent membrane through which the black iris is visible. By the end of the second day, a slight gray pigmentation on the future eyelids obstructs view of the iris; on the third day faint eye slits can be discerned. Development during the next few days is marked by an increase in pigmentation on the edges of the eye slits, and a deeper ingression of the slit itself. The increased size and subsequent outward pressure exerted by the eye causes a large bulge at the eye location on each side of the head.

The eyelids part from days 9 to 13, and the eye becomes visible. Sometimes, only one eye opens at a time, the opening of the other being delayed until the following day. Eyelids do not part completely until two or three days later. By the end of the second week, the eye resembles a shiny black bead bulging from the head. Further developmental changes are not noticeable.

Ears.—Newborn young have the ear pinnae folded anteriorly and fused with the skin of the head. During the second day and sometimes as late as the third, the ear pinnae become free and extend at right angles to the head, thus exposing the darkly pigmented skin which seals the external auditory meatus. The day after the ear pinnae have been freed, they come to lie close to the head in a more vertical position. At this time, the pinnae are mere fleshly knobs which are colored along the border by dark gray pigment.

The external auditory meatus opens on days 9, 10, or 11, and is followed by rapid development of the fleshy parts of the ear. Also noticeable is an increase in the density of the brown hairs growing along the edge of the ear. The majority of the mice studied by Layne (1959) had open auditory canals on the seventh day, but the opening was delayed as late as 10 days in some of his individuals.

External ear development after the first two weeks is limited to the pinnae becoming slightly ovate as they approach the adult condition.

Digits.—The lateral digits (digits 4 and 5 of each foot) are only partially fused at birth, whereas the remainder are fused from the base of the ill-defined claws to the proximal end of each digit. Usually,

the digits of the forefeet are more fused than their hind counterparts. "Well-separated" digits soon after birth are reported by Layne (1959). The difference in these observations might be attributed to individual variation or possibly to geographic variation. Layne's work was carried out in Florida, the southern limit of the subspecies range on the Atlantic coast, while the author's study was based on specimens from North Carolina, the northernmost state of the subspecies range on the Atlantic coast. Additional work is necessary to clear up these discrepancies.

Pelage.—Young at birth appear unpigmented, are pink, and have a translucent skin. Tiny white natal hairs on the back, neck, and head can be seen with the naked eye, but the hairs of the sides and venter require the use of a hand lens to be seen. All other parts of the body are naked, except the well-developed vibrissae which protrud from the blunt snout.

The dorsum becomes slightly pigmented on the day following birth. The rest of the body remains pinkish. The tail is bicolored due to the dark gray pigmentation on top and pink below. Pigmentation and the density of hairs increase markedly in the mid-dorsal and nape regions, until by the fifth day a brown tinge is conspicuous in the nape region. These changes are paralleled by an increase in the number of white hairs on the venter and on the legs to the base of the digits. Also, first noticeable on the fifth or sixth day is the presence of epidermal scales on the head and back.

At day 7 the brownish hair on the head and nape almost completely hides the underlying skin. The faded pink or almost white color of the belly skin readily shows through the sparse hairs on that part of the body. The skin becomes opaque by the end of the first week of development.

By the eighth day after birth, the brown-gray hairs of the back have covered the sides of the young and form a line of separation where they meet the white hairs of the belly. Sparse white hairs now cover the digits to their distal ends. The epidermal scales of the dorsum and flanks disappear by the eighth or ninth day.

Ten days after birth, the pelage is developed enough to be suggestive of the gray juvenile pelage of most members of the genus *Peromyscus*. The hairs exhibit a sheen and adhere closely to the contours of the body.

An increase in the density of the underfur is distinctly evident in all animals by the start of the second week. The number of guard hairs increases at a slower rate than the underfur hairs. Small traces of the adult ferruginous color usually make their first appearance on day 17 or 18 around the eyes and sides of the young.

During the fourth week, buff colored hairs are prominent on the venter. Also during this period, ferruginous hairs appear higher up on the sides between the forelegs and hind legs.

In further development, the pelage shows a replacement of the grayish juvenile hairs by the ferruginous-brown hairs of the adult.

Usually the rump is the first part of the back to be covered with the adult-type color. Next is the area from the rump to the shoulders. The patch of ferruginous hairs in the eye area gradually enlarges, replacing the gray around the cheeks and extending posteriorly until the molt is completed. A more detailed description of the molt in *Reithrodontomys* is given by Layne (1959).

GROWTH OF YOUNG EASTERN HARVEST MICE

Weight increments.—The daily mean weight increments from birth to 50 days of age for 24 laboratory-born harvest mice indicate an initial fast-growing phase during the first nine days, followed by an abrupt decrease in growth rate on the tenth day (Fig. 1). Daily incre-

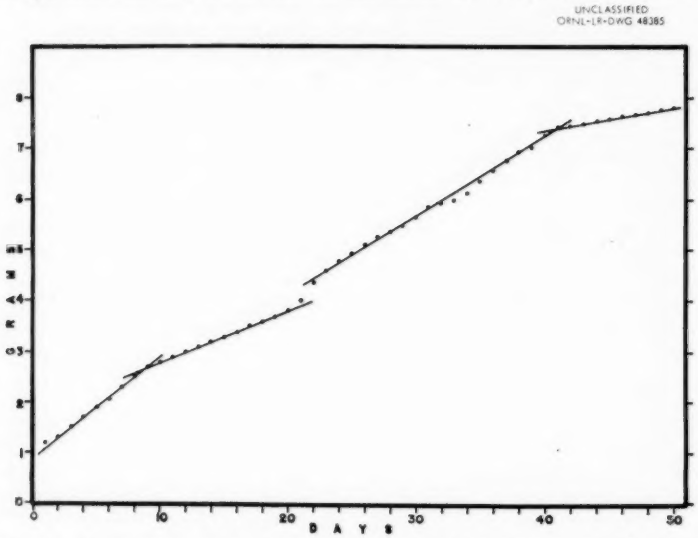


Fig. 1.—Daily mean weight increments showing four separate growth phases from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

ments of about equal magnitude are added from the tenth until about the twentieth day when a third growth phase begins and lasts until the fortieth day. The third growth phase exhibits a slope greater than the second, but not so great as the initial phase. A fourth growing phase, having a very gradual slope, reflects a reduced rate of growth from days 40 to 50. When weighing was discontinued at day 50, mice were still gradually increasing in weight.

During the first growth phase, the young are nurtured entirely on milk of the mother; however, both solid food and milk make up the diet during the second growth phase. Probably reduced lactation and the inability of the young to fully utilize solid food at this time results

in the decreased growth rate between days 9 and 21. A small amount of nursing may still be taking place by the twenty-third day after birth, but by this time the young are usually subsisting on solid food. All young are weaned by the end of the third week.

The ability of the digestive system to utilize fully the nutrients from solid foods is reflected in the increased growth rate from days 23 to 40. After day 40, daily weight increments are much reduced as the animals approach adult weight.

Linear growth.—Growth in total length is rapid for the first two weeks after birth but progressively tapers off during the third, fourth, and fifth weeks (Fig. 2). By the end of the seventh week, daily increments in total length indicate much slower growth.

The growth curves for the left hind foot (Fig. 3) and tail vertebrae (Fig. 4) are essentially parabolic. The hind foot approaches the adult size by the end of the third week. This rapid growth is correlated with other aspects of the biology of the young, for at this time young mice are being weaned and must forage around by themselves in search of food. By the beginning of the fifth week, the growth curve of the hind foot shows signs of being asymptotic. The linear growth of the tail does not begin to level off until the sixth week (Fig. 4).

A sigmoid-type growth curve (Fig. 5) is evident for the daily mean increments in ear length measured from ear crown to tip. The great-

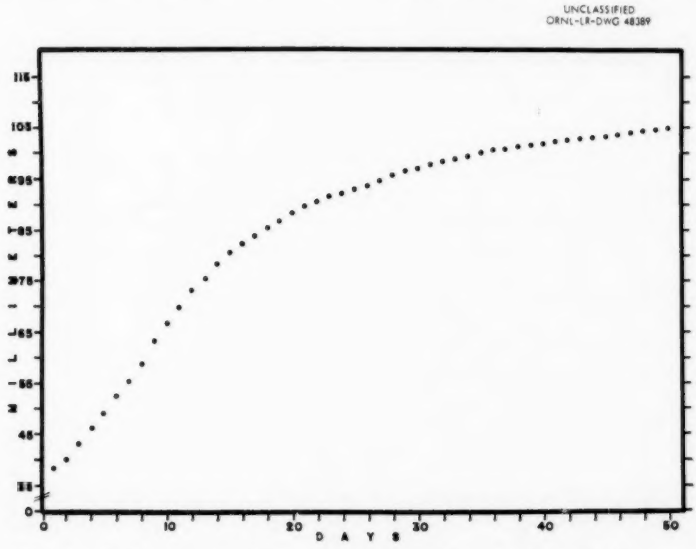


Fig. 2.—Daily mean total length increments from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

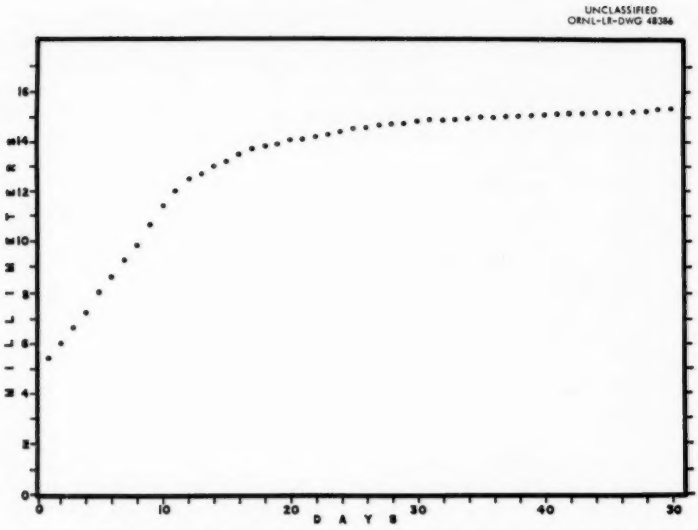


Fig. 3.—Daily mean length increments of left hind foot from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

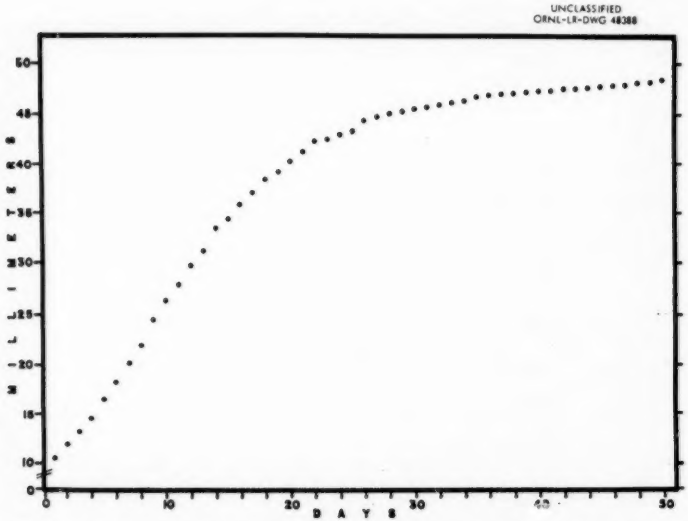


Fig. 4.—Daily mean length increments of tail vertebrae from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

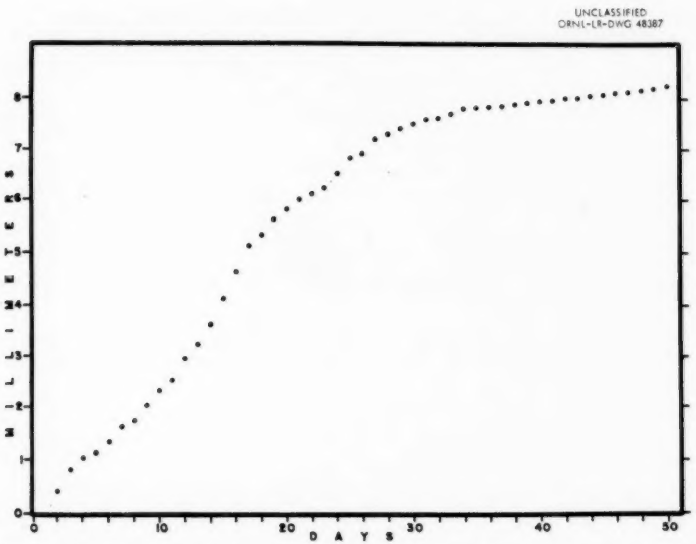


Fig. 5.—Daily mean ear length increments measured from ear crown to tip from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

est length increments occur from days 11 to 19 and are followed by a slowing of the growth rate until the increments of the fifth and sixth weeks are but a fraction of the increments during the fast-growing phase.

BEHAVIORAL PATTERNS OF EASTERN HARVEST MICE IN CAPTIVITY

Feeding habits.—The favorite food of laboratory animals was rolled oats. When rolled oats and other foods were mixed and placed in a container within the cage, the rolled oats were always eaten first. Seeds from a lawn mixture of Kentucky blue grass (*Poa pratensis*), red top (*Agrostis alba*), fescue (*Festuca* spp.), perennial rye grass (*Lobium perenne*), and white clover (*Trifolium repens*) were readily hulled and eaten. Mice were also maintained for a long time exclusively on the seeds of Korean lespedeza (*Lespedeza stipulacea*).

Occasionally a piece of apple or other succulent was placed in the cages along with the usual rolled oats or seeds. The succulent material was usually not eaten until after it had become partially dry. This may indicate that harvest mice in the wild obtain water primarily from dew and rain drops and do not utilize succulent vegetation. Other observations point to this too, because pieces of freshly cut green fescue stems and leaves were left untouched but the seeds from the same plants were eaten. Caged harvest mice seemed to prefer to satisfy their thirst by drinking from the water bottles which were always at

their disposal. Fresh fruits and vegetables were fed by Layne (1959) to his colony of Eastern harvest mice.

Harvest mice skillfully pick up tiny seeds in their mouths and transfer them to cupped forepaws. While eating, they sit on their hind quarters, leaving their front legs free for food manipulation. When a piece of rolled oats is being eaten, it is slowly rotated by the forepaws as the edge is chewed off. Rotation continues either until nothing is left or until any small piece which remains is discarded.

Food caches of rolled oats were noted in the corners of cages and nest boxes. This behavior was reported by Layne (1959) only for pregnant females. In the present study, food caches were not restricted to pregnant females.

Sex toleration.—Although males get along well with females, males rarely tolerate each other in the same cage. One instance was recorded in which an adult male killed another adult male on the second day the two were together. During this two-day period, the aggressor continually chased the other mouse about the cage, nipping it around the rump. When the mouse was found dead, it was badly chewed around its hind quarters and tail. Other males were often observed fighting, but none was killed.

Females are exceedingly tolerant of members of their own sex. During a six-week period in the summer of 1958, seven females were housed in one cage. They lived together in a single nest and were always observed to get along well together. When a single male is paired with a single female, toleration before pregnancy is equally as good.

Behavioral variation among individuals.—In general, harvest mice are highly excitable animals. Excited animals exhibited two signs. First there was a noticeable increase in external respiration, probably accompanied by an increased heart beat. Second there was a lateral whipping movement of a much stiffened tail, similar to the way a rattlesnake shakes its rattle. When the tail, moving with rapidity, touched the wooden cage or nest box, the resultant sound was comparable to the muffled noise of a woodpecker pecking on a tree.

Two adult male harvest mice were captured in March, 1958 and maintained for a period of time in separate cages. These two animals exhibited two extremes of behavior. One was very secretive and nervous, while the other was quite tame. The secretive mouse preferred to remain in its nest all day, coming out only at night when no one was in the laboratory. When discovered out of the nest, it would retreat rapidly into the nest box. This mouse would not voluntarily permit itself to be handled and tried to bite at every opportunity. On the other hand, the other mouse was often seen out of its nest during the day. One of its favorite daily pastimes was to perch on the hardware cloth side of the cage for periods of up to two hours with hardly any movements. On one evening it perched on the side of the cage

in a vertical position from 9:30 PM until midnight. This mouse would sit in my hand and allow itself to be petted. No attempts were made to bite or escape.

A third mouse had the habit of hanging onto the hardware cloth side of the cage and gnawing on the galvanized wire. After gnawing from 15 minutes to one-half hour each day for two weeks, it was halfway through the wire when it unexpectedly discontinued the activity.

Sanitation.—Cleanliness is an outstanding trait of *Reithrodontomys humulis*. Toilets were confined to the corners of the cages and were only rarely found in the nest boxes. There was however an occasional voiding of urine in a food tray as a mouse sat eating.

A great deal of time was spent by each mouse in washing and smoothing its fur. Particular care was taken to insure that each hair was glistening and in its proper place.

REFERENCES

AUDUBON, J. J. AND J. BACHMAN *Circa* 1854. The Quadrupeds of North America. George R. Lockwood. New York. 3 vols.

BRIMLEY, C. S. 1923. Breeding dates of small mammals at Raleigh, North Carolina. *J. Mammal.*, **4**:263-264.

FRANK, F. 1957. The causality of microtine cycles in Germany. *J. Wildl. Mgmt.*, **21**:113-121.

HALL, E. R. AND K. R. KELSON 1959. The Mammals of North America. The Ronald Press Company. New York. 2 vols.

HOLDING, B. F. AND O. L. ROYAL 1952. The development of a young harvest mouse, *Reithrodontomys*. *J. Mammal.*, **33**:388.

LAYNE, J. N. 1959. Growth and development of the Eastern harvest mouse, *Reithrodontomys humulis*. *Bull. Florida State Mus., Biol. Sci.*, **4**(2): 61-82.

SVIHLA, R. D. 1931. Notes on desert and dusky harvest mice (*Reithrodontomys megalotis megalotis* and *R. m. nigrescens*). *J. Mammal.*, **12**:363-365.

Occurrence of Subterranean Isopods in Epigean Waters[1, 2]

W. L. MINCKLEY
University of Louisville, Louisville, Ky.

ABSTRACT: *Asellus stygius* (Packard) was collected at 20 localities in epigean waters of Meade and Jefferson counties, Kentucky. Most observations were made in Doe Run, Meade County, where the species occurred frequently enough in the riffle habitat to be considered a consistent, but minor element of the epigean fauna. The species maintains populations in this environment numbering as high as 43 individuals per square foot.

INTRODUCTION

The occurrence of troglobitic organisms in the epigean environment is generally attributed to accidental displacement (Barr, 1960; and others). This is especially true of the highly modified cavernicolous asellids, with two species, *Asellus tridentatus* (Hungerford) (Leonard and Ponder, 1949; and Dexter, 1954) and *A. conestogensis* (Levi, 1949), being recorded from surface habitats. This paper describes the frequent occurrence of *A. stygius* (Packard) in surface waters of Meade and Jefferson counties, Kentucky. Most of the observations were made in Doe Run, Meade County, with additional material being collected from Otter Creek and "Morgan's Creek," Meade County, and Harrod's Creek, Jefferson County.

Dr. Gerald A. Cole, Arizona State University, assisted in the identification of the specimens of *A. stygius*. Dr. Louis A. Krumholz criticized the manuscript, and he and others of the University of Louisville assisted in the collection of data.

DESCRIPTIONS OF THE STREAMS

The four streams from which *A. stygius* has been collected contrast sharply in physical ecology. Doe Run is a large spring, with an average flow that exceeds 50 cubic feet per second, and with a resultant moderation of temperature extremes throughout. The creek flows primarily over rock substrata for about 10 miles, and enters the Ohio River about four miles upstream from Brandenburg, Kentucky. General descriptions of Doe Run, adequate for the purposes of this report, have been published elsewhere (Cole and Minckley, 1961; Minckley and Craddock, 1961).

The spring originating in Morgan's Cave, herein termed Morgan's Creek, is located in Otter Creek Park, Meade County, Kentucky. The

[1] Contribution No. 44 (New Series) from the Biology Department, University of Louisville, Louisville 8, Kentucky.

[2] This work was supported in part by the U. S. Atomic Energy Commission under Contract No. AT-(40-1)-2595, with the University of Louisville.

spring is small, with an average flow of about 30 gallons per minute; the spring creek extends for approximately one mile to enter the Ohio River near Rock Haven. The source is located high on a limestone bluff, with the stream descending through broken rubble to pass through a deeply incised, heavily vegetated ravine. The flow of Morgan's Creek is relatively constant. The heavy shade contributes to more or less stable conditions throughout the stream.

Otter Creek, located near Fort Knox, Kentucky, and flowing part of its length through the Fort Knox Military Reservation, is a larger stream than the two mentioned above, and is fed by surface water and small springs along its course. The creek is subject to radical fluctuations in flow, temperature, and turbidity, and these extremes occur much more frequently than in Doe Run or Morgan's Creek.

Harrod's Creek, Jefferson County, is similar to Otter Creek, but is somewhat larger. This stream is located in eastern Jefferson County, and flows directly into the Ohio River upstream from Louisville.

HISTORY OF COLLECTIONS

Asellus stygius was first collected in surface waters near the source of Doe Run in February 1959. At that time no intensive sampling was attempted, and the occurrence was thought to be fortuitous because of the proximity of the spring. On that date, examination of rubble in the mouth of the spring and to about 50 feet downstream produced 19 specimens. Intensive studies of the ecology of Doe Run were initiated in October 1959, and within two months *A. stygius* had been collected at all five of the permanent stations established on the creek, and a number of specimens were obtained at each of four additional localities. At this writing (February 1961), *A. stygius* has been repeatedly taken at the five sampling stations, and the total number of localities on the creek where it has been collected has been increased to 12. This total does not include three collections that were made inside of caves in the drainage. There seems little correlation between the collection sites and the location of caves from which the isopods could have been displaced. The creek basin has been thoroughly explored, thus precluding the occurrence of open caves at unknown places in the drainage; however, the possibility of fissures and undetected springs in the bed of the creek cannot be overruled. The numbers of specimens obtained at some of the localities strongly suggests that some populations are maintaining themselves in the surface environment.

The three additional streams in which *A. stygius* has been collected tend to substantiate the apparent independence of some populations from the true cave environment. The species has been taken in the surface portion of Morgan's Creek on three occasions (four collections have been made in the cave and stream, all of which included specimens from inside the cave). Specimens were obtained twice from the creek about 200 yards above its confluence with the Ohio River, and three times in that portion within 300 yards of the cave. The

records from Otter and Harrod's creeks each are based on single collections. The four small specimens from Otter Creek were all taken beneath the same stone in June, 1960, and two adults were obtained in a similar habitat from Harrod's Creek in October, 1960.

HABITAT AND NUMBERS

In caves, I have found *A. stygius* usually on the under side of flat stones and other debris. Sometimes the species has been seen walking openly on flat rock bottoms and on the walls of solution channels, and it is often found to be most abundant in small solution pools high above the existing water levels in a given cave.

In the surface waters of Doe Run the species is usually found beneath the larger stones on riffles, and in areas that actually approximate the cave environment. However, in many instances, the species was found on rocks less than six inches in diameter, which were loosely associated in relatively swift water. These types of habitat were similar to the areas inhabited by *A. stygius* in Morgan's, Otter, and Harrod's creeks, and are analogous situations to those described for the epigean occurrences of other species (cited above).

Another common habitat in Doe Run, especially in the lower section of the creek, consists of loosely constituted gravels. Thirty specimens were collected in less than half an hour on a gravel bar by carefully digging into the substratum and examining each small stone. The isopods were found to a depth of about six inches, and were typically clinging tightly to the lower surface of the stones, or were deep inside cracks or other irregularities.

The most unique habitat of this species in Doe Run is worthy of a more detailed description. The middle section of the creek includes an area of marl deposition. In this area many of the riffles appear to be bedrock, which, on closer examination, proves to be a recently formed (and currently forming) conglomerate of rubble and gravel cemented by marl. Repeated sampling of this habitat failed to produce any isopods until by chance I broke through the marl slab in the course of sampling with a square-foot Surber sampler. This collection included eight individuals of *A. stygius*. Further examination by hand revealed a large population of the species beneath the slab, and beneath other similar slabs throughout the marl area. In this case it appears that the isopods colonized a "cave" habitat that was formed in the epigean waters.

It is noteworthy that in all cases where *A. stygius* was collected in Doe Run there was consistantly a moderate to rapid current and consequent lack of siltation. Specimens kept in containers that were filled with silty water soon became incapacitated. Apparently the suspended particles entangle with the profuse setation, and thus the presence of silt may limit the spatial distribution of the species to areas of pronounced current.

I have no actual quantitative data on the numbers of *A. stygius* in Doe Run per unit area; however, some general estimates may be

made on a "number per rock" basis converted to the number per square foot of rock substratum. The maximum number of individuals found on a single stone was 43 — the stone measured approximately 10 by 14 inches. The average number of specimens for three collections from Doe Run was about four per square foot of surface, with the range from none to 43 (based on the examination of 60 stones larger than six inches in diameter). In the collections made in loose gravel the average number of individuals per square foot was about eight; however, many could have been overlooked. In the latter habitat the individuals averaged smaller in size than in other areas; however, sizes varied from 4 to 10 mm in length (excluding antennae and uropods) at most localities. As noted above, many specimens were taken from beneath marl slabs, but because of the current and the required breakage of the substratum, no estimates can be made as to the numbers present.

Three other asellids occur in Doe Run, and all of these have been taken in association with *A. stygius* at one time or another. These are *Lirceus fontinalis* (Rafinesque), *Asellus brevicaudus* Forbes, and another *Asellus*, which is now under investigation by Miss Barbara A. Walker of this department. The latter form is most abundant in the creek, and has been commonly collected beneath the same rock as *A. stygius* at two of the five permanent stations and at other localities.

REFERENCES

BARR, T. C., JR. 1960. Introduction. p. 1-9. *In* Symposium: speciation and raciation in cavernicoles. *Am. Midl. Nat.*, **64** (1): 1 - 160.

COLE, G. A., AND W. L. MINCKLEY 1961. A new species of amphipod crustacean (genus *Gammarus*) from Kentucky. *Trans. Am. Micro. Soc., in press.*

DEXTER, R. W. 1954. A record of the blind isopod, *Asellus tridentatus*, from an open stream habitat. *Am. Midl. Nat.*, **52** (1): 256.

LEONARD, A. B., AND L. H. PONDER 1949. Crustacea of eastern Kansas. *Trans. Kansas Acad. Sci.*, **52** (2): 168-204.

LEVI, H. W. 1949. Two new species of cave isopods from Pennsylvania. *Notulae Nat.*, **220**: 1-6.

MINCKLEY, W. L., AND J. E. CRADDOCK 1961. Active predation of crayfish on fishes. *Prog. Fish Cult.*, **23** (3): 120-123.

A New Genus of Fossil Salamander from North America

WALTER AUFFENBERG
University of Colorado, Boulder

ABSTRACT: A new genus and species of fossil salamander, *Opisthotriton kayi*, from Niobrara County, Wyoming, Lance formation, Upper Cretaceous, is described. On the basis of the structure of the centrum, *Opisthotriton* is, at present, best regarded as a salamandrid. However, certain features of the available vertebrae exhibit peculiarities encountered in this family as represented at the present time. The genus may eventually be assigned to the *Plethodontidae*, or to an extinct family. Most important is that the recognition of this genus and species establishes the presence of the suborder Salamandroidea in the New World during the Mesozoic. An additional specimen from the Eagle Coal Mine, Bear Creek, Montana, Lower Paleocene is referred to the same genus.

During the past few years several distinctive opisthocoelous salamander vertebrae from the Mesozoic and Cenozoic of North America have come to my attention. Comparison with other known fossil and Recent salamanders indicate sufficient dissimilarity to warrant the description of a new genus. The material constitutes one of the earlier records of fossil salamanders in the world, and provides additional information regarding the composition of the urodele fauna of the Cretaceous of North America.

I wish to thank Dr. M. Graham Netting and Mr. Leroy Kay, Carnegie Museum, for allowing me to study the fossil salamanders in their care, and to Dr. Alfred S. Romer and Mr. Henry Seaton, Museum of Comparative Zoology, for the opportunity of reporting on specimens in that collection.

By far, the most salient single character exhibited by the available specimens is the well-developed opisthocoelous condition of the vertebrae. Only the Salamandridae, and a few genera of the Plethodontidae have vertebrae of this general type.

Soler (1950) has shown that, in the Recent salamanders, opisthocoely may be of two basic types; i.e., (1) "hemicoelous," in which the anterior half of the notochordal canal is solid bone, and (2) "pseudocoelous," in which the notochordal canal is hollow for almost its entire length, but covered anteriorly by an ossified or cartilaginous cap. Partly on the basis of the opisthocoelous condition of the vertebrae Soler resurrected Cope's Desmognathidae (Cope, 1866). Moore (1900), on the other hand, had considered opisthocoely as a character of little phyletic value, and had placed Cope's Desmognathidae in the Plethodontidae.

According to Soler, the Desmognathidae includes the Recent genera *Desmognathus* and *Leurognathus*, both of which are hemicoelously opisthocoelous.

Pseudocoelous opisthocoely of the type in which the anterior cap is osseous, occurs in all members of the family Salamandridae, as well as in the Recent plethodontid genus *Thorius*.[1] Pseudocoelous opisthocoely of the type in which the anterior cup becomes covered or filled with a cartilaginous cap or ball, occurs in older specimens of some plethodontid salamanders. However, as indicated by Soler, this is a secondary condition, and quite different from that observed in pseudocoels in which the cap is bony throughout life.

The fossil opisthocoelous vertebrae are provided with a condyle which can hardly be considered to have been cartilaginous in life, due to the absence of any shrinkage of the cap. However, it is possible that under the special conditions of preservation the cap would not have contracted after death as it does in skeletal preparations of recent cartilaginous pseudocoels.

Since the condyle is considered to have been bony in life the question then arises, is the centrum like that found in the hemicoelous, or the osseous pseudocoelous types?

By sectioning Recent salamander centra in the median sagital plane Soler was able to compare the internal structure of the condyle and the notocordal canal. None of the fossil vertebrae were actually sectioned, but one specimen is broken in such a manner that it is possible to see the internal structure of the centrum and the condylar process. The latter is obviously hollow, being covered by a bony (?) cap. The notochodal canal is broad and open for almost its entire length. On this basis the fossils are tentatively referred to the family Salamandridae. However, the possibility still remains that the vertebrae belong to a plethodontid possessing a bony cap, such as that found in *Thorius*. Or, the cap here interpreted as having been bony in life, may have actually been cartilaginous, in which case the vertebrae most closely approach those in some of the Recent plethodontids, such as *Gyrinophilus*. On the other hand, the large size of the fossil vertebrae, as well as certain other characters, may suggest that the fossils should be placed in a new and separate family and not forced into a taxon which will not readily receive it on the basis of our present knowledge.

A number of important studies have been published on fossil urodele remains from Europe, where the earliest salamandrid is reported from the Paleocene. In North America a member of this family has been described from the Oligocene of Oregon (*Palaeotaricha* van Frank, 1955). The vertebrae described below are quite different from any previously reported, either from the New or Old Worlds. The material originates from both Cretaceous and Paleocene strata of western United States. It is placed in a new genus:

[1] Cope (1869) had already recognized the peculiar position of *Thorius* in proposing the family Thoriidae. Later (1873) he revised his concept of the entire group and reduced the Thoriidae to subfamily status under the Desmognathidae. In the present paper the recent checklist (Schmidt, 1953) is followed in placing *Desmognathus* and *Leurognathus* in the Desmognathinae.

Opisthotriton n. gen.

Genotype.—Opisthotriton kayi n. sp.

Diagnosis.—Vertebrae opisthocoelous, larger than any other salamandrid or plethodontid vertebrae known, either fossil or Recent. Hypapophysial keel more strongly developed than in Recent genera of Salamandridae or Plethodontidae. Basipophysial accessory processes strongly developed near the postero-ventral margin of the centrum. As far as is known, similar processes, when present in Recent salamanders, are not located in the same position. Neural arch without the well-developed neural spine observed in many salamandrids, not unlike that in many plethodontids.

Opisthotriton kayi n. sp.

Type.—Carnegie Museum Cat. Vertebrate Fossils No. 6468, a middle trunk vertebra collected by J. B. Hatcher, 1900 (Fig. 1).

Type locality and horizon.—Niobrara County, Wyoming; Lance formation; Upper Cretaceous.

Referred material.—All from the same locality and horizon. Carnegie Museum No. 6466, four fragmentary vertebrae from a smaller individual. Carnegie Museum No. 6468, a complete maxillary, several fragmentary skull elements and two complete atlantes. Museum of Comparative Zoology No. 2813, a single large trunk vertebra.

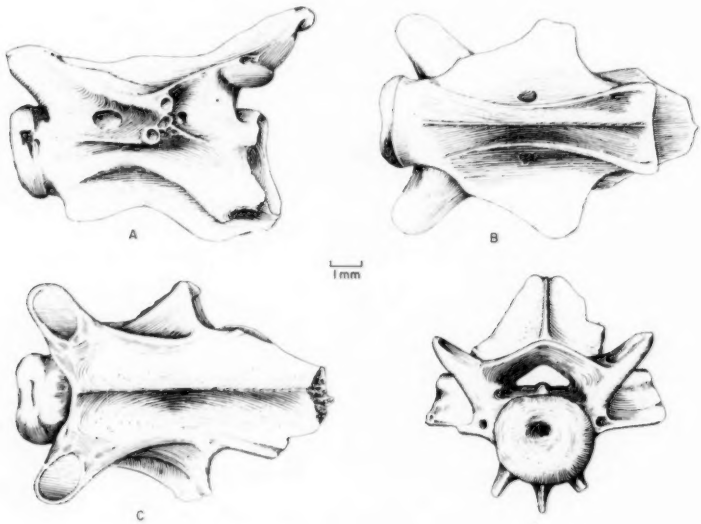


Fig. 1.—Type. *Opisthotriton kayi* nov. gen. et sp., Carnegie Museum No. 6468. A, Lateral; B, Ventral; C, Dorsal and D, Anterior Views. Niobrara County, Wyoming, Lance formation, Upper Cretaceous.

Diagnosis.—As for the genus.

Description.—A middle trunk vertebra (CM 6468) in which the right prezygapophysis and posterior portion of the neural arch are broken away. The measurements (in mm) are as follows: length of centrum along midventral line 8.0; width of the narrowest part of the neural arch from the outer edge of one zygapophysial ridge to the outer edge of the other 3.7; height from the lower margin of the centrum to a line drawn between the outer edges of the prezygapophysial articular facets 4.9.

The vertebra is pseudocoelously opisthocoelous, with a very obvious and well-developed condyle. A notochordal depression is present in the center of the condyle. A median hypapophysial keel is very evident, extending from the anterior to the posterior margins of the centrum. On either side of the hypapophysial keel there are two conspicuous and well-developed basipophysial accessory processes which are best developed posteriorly. Anteriorly they become ridge-like, extending almost to the anterior edge of the hypapophysial keel. A single nutritive foramen is located on either side of the centrum at its union with the base of the transverse process. Condyle circular, flattened antero-posteriorly, with a central depression. Posterior cavity of the centrum rounded, not compressed. Transverse processes broken, but with two distinct rib articulations, connected by a vertical septum. The anterior portion of the lower lamina of the transverse process begins just below and behind the base of the postzygapophysial buttress. It continues posteriorly to near the posterior margin of the centrum. The dorsal lamina is continuous with the interzygapophysial ridges. A large foramen for the vertebrarterial artery is present between the dorsal and ventral laminae of the transverse process just in front of its base. A second foramen, for a spinal nerve, is located just posterior to the base of the transverse process. The prezygapophysial articular facets are oval, directed outwards and forwards from above, and upwards and slightly inwards from the front. The neural arch is depressed, sweeping upwards posteriorly, with a low keel-like neural spine, which is slightly higher posteriorly. The neural canal is low and wide.

Variation.—The four small fragmentary referred vertebrae (CM 6466) provide some information as to both inter- and intra-columnar variation, since their smaller size suggests a different individual than the one represented by the holotype.

All the elements are considerably smaller than the type, and are apparently from an animal about one half the size of the one of which the type vertebra is available. One of these specimens is a middle trunk member. It differs from the type in being much smaller, more obviously depressed, and somewhat more elongate when viewed from above. The hypapophysial keel and the accessory basipophysial processes are less well-developed than in the type. Another vertebra of this series is quite unusual in that the basipophysial accessory processes are extremely well developed. Posteriorly they are twisted

so that their free ends are not parallel with the median sagittal plane. Instead, the flattened, blade-like free ends are directed downwards and backwards, with the flat surface facing downwards and forwards; i.e., they are directed in nearly a transverse plane, though oblique. The free ends of the processes are much longer than in the type, and extend below the ventral lip of the cavity of the cotyle. Whether or not this element represents a vertebrae from near the sacral area is unknown. It might even be a vertebra from the anterior caudal series, although the transverse processes are more like those of the dorsal elements. There is little reason to believe that it represents a second species of *Opisthotriton,* since its peculiarities are simply extensions of a development observed in the type. The chief differences lie in the greater length of the free ends of the accessory basipophysial processes and a flexure of their posterior ends so that they come to be disposed more transversely than parallel to the sagittal plane. Until proven otherwise, the vertebra is best referred to the posterior part of the presacral portion of the column. Similar processes, though located anteriorly on the centrum, are present in the dorsal vertebrae of some caecilians. Their exact function seems unknown, though similar structures in certain extinct amphibians and some fishes are thought to be functionally important in limiting excessive lateral movement. This is particularly important in swimming vertebrates whereby greater efficiency in locomotion is attained by making the body more rigid and thus increasing length of the wave of the swimming movements. Similar structures, though much smaller, and located at the anterior end of the centrum are also found in at least two recent salamander groups; the Sirenidae and the Amphiumidae, both highly specialized for swimming through water. On this basis it is presumed that *Opisthotriton* was a very large aquatic form (to three feet?). The appendicular skeleton was probably reduced. More extensive functional and ecological considerations must await the discovery of a more or less completely articulated skeleton.

The two remaining vertebrae in the series are so fragmental as to preclude comment other than that their general determinable shape indicates they are conspecific with the two small vertebrae briefly described above.

The Museum of Comparative Zoology specimen (No. 2813) is about the same size as the type, but unique in several features, so that it is described in full below. It is here interpreted as an anterior vertebra on the basis of the great development of the hypapophysial keel. The basipophysial accessory processes are less strongly developed than in the type, and the neural spine is higher. The prezygapophyses are not as divergent when viewed from the front or from above.

Unfortunately, the right prezygapophysis and the posterior portion of the neural arch are broken away. As in the type, the vertebra is pseudocoelously opisthocoelous, with a well developed condyle. A median hypapophysial keel is very evident. On either side of the keel on the posterior part of the centrum are two conspicuous and well

developed basipophysial accessory processes, which become weaker anteriorly. There are no nutritive foramina between these processes and the median keel. A single nutritive foramen is located on either side of the centrum at its union with the transverse process. The condyle is circular, with a central depression. The posterior cavity, or cotyle, is rounded, not compressed. The transverse processes are provided with two distinct rib articulations, connected by a vertical bony septum. The anterior portion of the lower lamina of the transverse process begins just below the middle of the buttress of the prezygapophysis, and continues posteriorly to near the posterior edge of the centrum. The dorsal lamina is continuous with the interzygapophysial ridges. Two large foramina occur on the centrum between the dorsal and ventral lamina, both immediately anterior and posterior to the base of the transverse process. The prezygapophysial articular facets are apparently oval, directed outwards and forwards from above, and upwards and inwards from the front. The neural arch is depressed, raised upwards posteriorly, with a keel-like neural spine. The neural canal is low and wide. The specimen is illustrated in Figure 2.

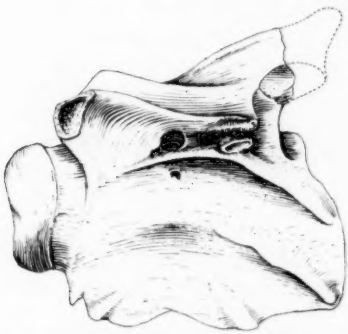


Fig. 2.—Museum Comparative Zoology No. 2813, a more anterior vertebra referred to *Opisthotriton kayi* nov. gen. et sp., lateral view. Same locality and horizon as the type.

In addition to the vertebrae mentioned above, two atlantes are available which are referred to this species (CM 6468). In general shape they are less similar to the same element in the Recent Salamandridae than they are to the atlantes of some plethodontids (Fig. 3).

The condylar articulations are rounded and well-separated by a rather thin horizontal septum-like process. The neural arch pedicels are fairly high and narrow; bent slightly medially near their dorsal edge. The neural arch is capacious, being almost as broad as high. The odontoid process is present, though not greatly developed. It is subtriangular from the front, obtusely triangular from the side, and projecting farthest anteriorly near the antero-dorsal edge. The centrum is short, not compressed or with aberrant processes. From below

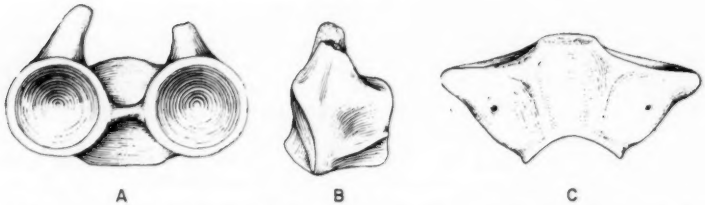


Fig. 3.—One of two available atlantes referred to *Opisthotriton kayi* nov. gen. et sp., Carnegie Museum No. 6468. Same locality and horizon as the type.

it is triangular, broadly truncated posteriorly. The centrum articular cavity produces a definite concave posterior edge on the ventral surface of the centrum. Laterally a slight ridge runs from the ventro-lateral edge of the condylar facet posteriorly and slightly dorsally to the postero-lateral edge of the centrum. The ridge apparently separates the origins of the muscle fibers of the *M. subvertebralis* and the superficial portion of the *M. levator mandibulae anterior.*

An available right maxillary (CM 6468) referred to this genus (Fig. 4) is long and narrow, with the processes of the *pars facialis* located near the anterior end of the element. The anterior parts of

Fig. 4.—Right maxillary, lingual view, referred to *Opisthotriton kayi* nov. gen. et sp., Carnegie Museum No. 6468. Same locality and horizon as the type.

the *pars dentalis* is broken off. The former is roughly trapezoidal in shape and directed slightly anteriorly. At the lingual dorsal border are several knob-like protuberances, separated from the *pars dentalis* by a shallow groove. This groove is more obvious anteriorly than posteriorly. It is here interpreted as the naso-lacrimal duct. The element is provided with fifty-one teeth and/or alveoli. The teeth are shorter anteriorly, gradually increasing in size posteriorly. In cross section they are hollow, and slightly compressed antero-posteriorly.

The tip of a left dentary (CM 6468) is referred to the same species. There are alveoli for eight teeth. There are five foramina in a row on the lingual surface.

Opisthotriton sp.

In addition to the species described above, a second seems represented by a single vertebra (Carnegie Museum No. 6469) from the Eagle Coal Mine, Beartooth Creek, Montana, Lower Paleocene. The specimen is too fragmentary to warrant description as a new species.

As in *Opisthotriton,* the vertebra is opisthocoelous and quite large

when compared to most Recent salamanders. It differs from *Opisthotriton kayi* in lacking a well-developed hypapophysial keel, though this structure may have been worn away. The specimen has been badly eroded. The neural arch is depressed, but considerably raised posteriorly. The accessory basipophysial processes are present posteriorly, though they seem to be less well developed than in *O. kayi*. From above the element seems to lack strongly developed interzygapophysial ridges, but these too may have been worn away. In all other regards the specimen is essentially the same as that of the type and referred vertebrae of *O. kayi*.

The opisthocoelous centrum and the posteriorly placed accessory basipophysial processes suggest a close relationship to *Opisthotriton*, and the specimen is tentatively placed here until more complete material becomes available. Figure 5 illustrates the vertebra, slightly reconstructed.

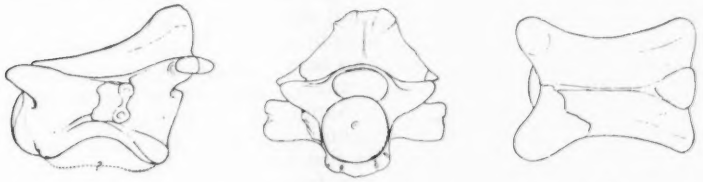


Fig. 5.—A single vertebra (Carnegie Museum No. 6469) from the Eagle Coal Mine, Beartooth Creek, Montana, Lower Paleocene referred to *Opisthotriton* sp.

DISCUSSION

Perhaps the most important single contribution to our knowledge of paleo-herpetology provided by these specimens is the establishment of the presence of the suborder Salamandroidea in the New World during the Mesozoic. However, the familial assignment of the fossils is not definitely established.

Cope (1876) described two genera of urodeles from the Lance, *Scapherpeton* and *Hemitrypus*. The types ha e apparently been lost, at least temporarily, and the relationships of these two genera are not at all clear. Herre (1950) indeed doubted the existence of any true salamanders in the Mesozoic, placing Cope's genera in the Palaeourodeloidea, a poorly defined group at best. The present material contradicts the view that the true salamanders were not present in the Cretaceous. In addition, Goin and Auffenberg (1957) have shown that the suborder Meantes was already well-established in Lower Cretaceous time.

As pointed out above, on the basis of the structure of the centrum, *Opisthotriton* is, at present, seemingly best regarded as a salamandrid. However, certain features of the vertebrae exhibit peculiarities not

encountered in this family as represented at the present time. The genus may eventually be assigned to the Plethodontidae, or to an extinct family.

The very well-developed hypapophysial keel is one such peculiar feature. A structure of this type, developed to the degree in which it occurs in *Opisthotriton* is, to my knowledge, lacking in all Recent salamanders. It is fairly well-developed in certain highly modified swimming forms, such as *Siren* and *Amphiuma,* but not to the extent that it is in the fossil form. This might suggest that *Opisthotriton* was also a highly modified swimming form. (The importance of the unique keel as a tool in attempting to establish the degree of relationship to any modern group is, at present, unknown.) Of considerable more importance is the fact that the position, and the degree of the development of the accessory basipophysial processes are suggestive of a highly modified aquatic existence, in which efficient swimming played a major role. Herre and Lunau (1950) direct attention to similar structures (incorrectly termed hypapophyses) in *Dehmiella* from the Miocene of Europe. Largely on this basis they place *Dehmiella* in the Plethodontidae, which seems warranted in view of our present knowledge of the osteology of urodeles. Similar processes are found in several genera of plethodontids, including *Eurycea, Pseudotriton* and *Desmognathus* among others. The first two are frequently considered as more primitive members of the family. The processes are never found in Recent salamandrids as far as is known. When present in ambystomids, sirenids, amphiumids and even caecilians they are located at the anterior edge of the centrum, and are never as well-developed. *Dehmiella* surpasses all known modern representatives of the Plethodontidae in the development of these structures, though in *Opisthotriton* they are developed even more strongly. *Geyeriella,* from the Paleocene of Europe, a genus considered by Herre (1950) to be a primitive forerunner to the plethodontid salamanders, seems to have these processes very much reduced.

The referred atlantes are relatively simple, and similar to those found in salamandrid genera. They do not possess the aberrant processes found in most plethodontids.

The referred maxillary is considered primitive on the basis of its great length and the more anterior position of the *pars facialis.* The Salamandridae possess longer maxillae than do the Plethodontidae. The anterior opening of what is believed to be the nasio-lacrimal duct in the fossil maxillary is also worthy of comment in that the duct occurs in all Recent salamandrids and plethodontids, with the exception of the Desmognathinae (Wilder, 1913).

Dunn (1926) has postulated that the plethodontid salamanders arose in the New World from a salamandrid stock. The genus *Opisthotriton* (if the tentative familial assignment is correct) represents the earliest salamandrid reported so far. However, it is highly possible that in *Opisthotriton* we have represented a form phyletically intermediate between the two families. The European Paleocene

Geyeriella may thus represent a side line of the main evolutionary sequence leading to the Plethodontidae; which might explain some of its peculiarities. *Dehmiella* seemingly represents the first known true plethodontid and thus conforms with the general phenomenon of faunal "modernization" during the early Miocene.

If the plethodontids originated in the New World from a salamandrid type, and a somewhat intermediate form is present in the Upper Cretaceous, the Salamandridae must represent a very ancient lineage. Fossils of this family, much older than those now available, are thus to be expected.

REFERENCES

COPE, E. D. 1866. On the structures and distribution of genera of the arciferous anura. *J. Acad. Nat. Sci. Phila.* **6**:67-112.

———1869. A review of the species of the Plethodontidae and Desmognathidae. *Proc. Acad. Nat. Sci. Phila.*, pp. 93-118.

———1876. On some extinct reptiles and batrachia from the Judith River and Fox Hills beds of Montana. *Proc. Acad. Nat. Sci. Phila.*, pp. 340-359.

———1893. Second addition to the knowledge of the Batrachia and Reptilia of Costa Rica. *Proc. Am. Philos. Soc.*, **31**:333-347.

DUNN, E. R. 1926. The Salamanders of the Family Plethodontidae. Smith College 50th. Anniversary Publications, 441 p.

GOIN, C. J. AND W. AUFFENBERG 1957. A new fossil salamander of the genus *Siren* from the Eocene of Wyoming. *Copeia*, **1957** (2):83-85.

HERRE, W. 1950a. Der derzeitige Stand unseres Wissens über die fossilen Urodelen, zugleich einige Kritische Bemerkungen über *Boomgardia salamandriformis* v. Huene *Neues Jahrb. Geol.* Paläontol., Monatschriebungen, 1950, pp. 19-25.

———1950b. Schwanzlurche aus dem Paleocän von Walbeck. *In* Neue Ergebnisse und Probleme der Zoologie (Klatt-Festschrift). Leipzig, Geest und Portig, pp. 286-301.

———, AND H. LUNAU 1950. Neue fossil Schwanzlurche aus dem Burdigalium. Neues Jahrb. Geol. Pälaontol., Monats hriebungen, 1950, pp. 247-252.

MOORE, P. J. 1900. Post-larval changes in the vertebral articulations of *Spelerpes* and other salamanders. *Proc. Acad. Nat. Sci. Phila.*, pp. 613-622.

SCHMIDT, K. P. 1953. A checklist of North American amphibians and reptiles. American Society of Ichthyologists and Herpetologists. University of Chicago Press: Chicago, Ill. p. 1-366.

SOLER, E. I. 1950. On the status of the family Desmognathidae. *Univ. Kansas Sci. Bull.* **33**(12):459-480.

VAN FRANK, R. 1955. *Palaeotaricha oligocenica*, new genus and species, an Oligocene salamander from Oregon. *Breviora*, (45):1-12.

WILDER, I. W. 1913. The life history of *Desmognathus fusca*. *Biol. Bull.* **24**:251-343.

Liatris provincialis, sp. nov., (Compositae), Endemic in Western Florida

R. K. GODFREY[1]
Department of Biological Sciences,
Florida State University, Tallahassee

ABSTRACT: *Liatris provincialis* is newly described from western Florida. It is allied with the three species of Series *Pauciflorae* and is most nearly like *L. chapmanii*. *L. provincialis*, so far as now known, is restricted to Franklin and Wakulla counties, Florida. (Illustrated.)

Gaiser (1946) in her revision of the North American genus *Liatris* states that of the thirty-two species recognized by her the largest number for a single state, 12, occurrs in Florida. Three of the twelve are endemic in Florida: *L. garberi* A. Gray, *L. pauciflora* Pursh, and *L. laevigata* Nutt. *L. garberi* and *L. laevigata* are restricted to peninsular Florida, whereas, *L. pauciflora* occurs generally across the northern part of the state and in the upper peninsula.

The distinctiveness of the plant described below was first noticed when it was observed in great abundance on sand dunes along the Gulf of Mexico between Lighthouse Point and Peninsular Point, Franklin County. There it occurred from the crest of the fore dunes shoreward on more stabilized dunes and into the evergreen oak-sand pine scrub adjacent. This area is a small narrow peninsula more or less paralleling the mainland on the seaward side of Alligator Harbor and is sometimes referred to as Alligator Peninsula. Later the plant was found to occur in evergreen oak-sand pine scrub along the coast from nearby Ochlockonee Bay generally southwestward to Carabelle and a little beyond, a distance of about 30 miles; also on sandy ridges of turkey oak-longleaf pine about two miles back from the coast in this vicinity and for about two miles north of Ochlockonee Bay in the vicinity of Panacea. Diligent search in areas of coastal dunes and evergreen oak-sand pine scrub near the Gulf westward of the Apalachicola River and on sandy ridges of turkey oak-longleaf pine elsewhere throughout the Florida Panhandle failed to reveal any other places of occurrence for this new *Liatris*.

Liatris provincialis Godfrey, sp. nov.
Fig. 1

Liatris chapmanii affinis, sed capitulis (plerumque lato-divaricatis nec anguste adscendentibus) flosculisque minoribus. Cormi variabilis globosi vel ovales vel unco-elongati. Caules solitarii vel plures ad 8 dm alti simplices vel pauci-vel multiramosi striati dense breviterque

[1] This investigation was supported (in part) by a research grant, RG-6305, to the author from the Division of General Medical Sciences, Public Health Service.

cinereo-pubescentes vel raro subglabri. Folia numerosa in ambitu glabra, inferiora lineari-oblanceolata, gradatim in superiora minora linearia transeuntia. Capitula sessilia vel rarius breviter pedunculata sat distantia plerumque divaricata vel leviter adscendentia ca. 12-15 mm longa plerumque 3-flora. Involucra cylindrica vel subturbinata; phyllariis glanduloso-punctatis apice purpureis margine scariosis et cilatis, exterioribus ovatis breviter acutis vel longe acuminatis, interioribus lineari-oblongis breviter acuminatis. Pappi setae barbellatae 7-8 mm longae. Corollae tubus 6-7 mm longus, intus leviter pilosus basin

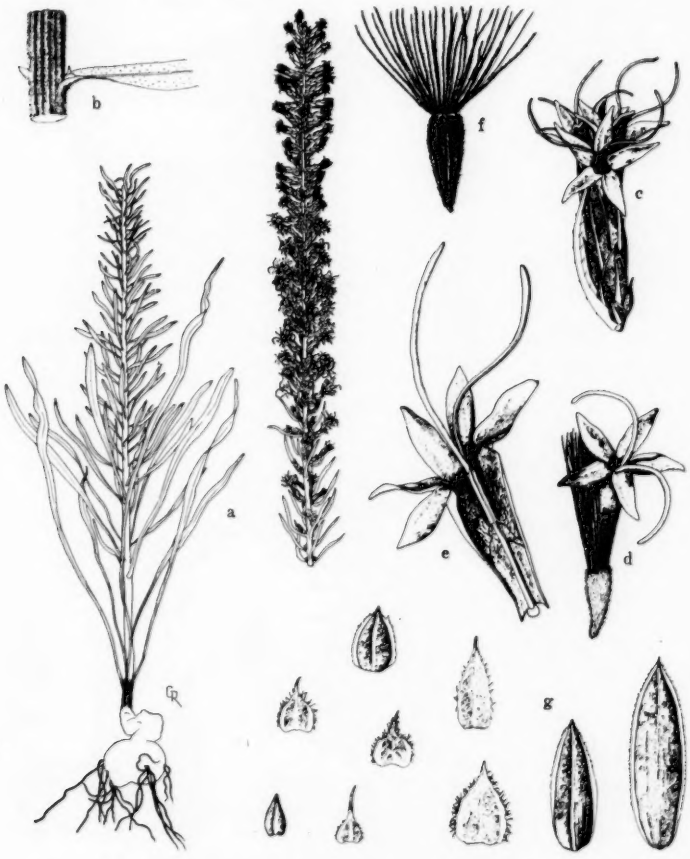


Fig. 1.—*Liatris provincialis:* a, habit; b, small portion of stem with a leaf base; c, head; d, flower; e, portion of flower with corolla slit longitudinally and spread open; f, achene; g, a representative series of phyllaries.

Additional specimens.—Franklin County: turkey oak-longleaf pine sand ridge, between St. James and the Ochlockonee River, September 16, 1960, *Godfrey 60282; Wakulla County:* turkey oak-longleaf pine ridge, ca. ¾ mile N of Panacea, September 16, 1960, *Godfrey 60283;* sandy scrub at Panacea, September 8 - 10, 1955, *Thorne* and *Davidson 17286.*

Liatris chapmanii T. and G., (Fig. 2), which this proposed new species most closely resembles, occurs both on sandy ridges of turkey oak-longleaf pine and in some areas of evergreen oak-sand pine scrub throughout the Florida Panhandle (as well as eastward and southward and with a single record for Decatur County in southwest Georgia). I have not ever observed it on coastal dunes nor have I seen it within the very limited range of *L. provincialis* even though, except for the dunes, the two species occupy what appear to be the same habitat types.

Liatris provincialis appears to be allied with the three species of Series Pauciflorae as delimited by Gaiser (1946) and is more nearly like *L. chapmanii* than to either of the other two, *L. secunda* Ell. and *L. pauciflora,* which are more similar to each other than either is to *L. chapmanii.* The one character possessed by *L. provincialis* which is not given as characteristic of the other members of Series Pauciflorae is that of ciliolate phyllaries. This is not here interpreted as significant in regard to the delimitation of the Series for its members do seem to form a natural group despite this species not having "read the book." As a matter of fact some of the phyllaries of *L. chapmanii* are ciliolate on some specimens.

Superficially and even at a distance *Liatris provincialis* can be distinguished from *L. chapmanii.* The heads of the former, at full anthesis, extend outward at right angles from the axis and are distant enough from each other so that the inflorescence has a decidedly interrupted appearance. This characteristic is somewhat obscured in pressed and dried specimens but still contrasts with the arrangement of the heads of *L. chapmanii* which are rigidly ascending, appressed to the axis and to each other, overlapping, and make the spike appear as a narrow, continuous cylinder. This difference is striking. The leaves of *L. provincialis* are not pubescent, those of the other are usually abundantly clothed with short stiff hairs. Most of the other features by which the two are distinguished are quantitative characters of the heads and flowers yet these features seem to be constant and some of them relatively large. The heads of *L. chapmanii* are longer (18-20 mm *vs* 12-15 mm) and somewhat broader although the breadth is difficult to specify because it depends at what stage of development the measurement is taken. The pappus is 11 mm long in *L. chapmanii* and 7-8 mm in the other. The corolla tube and lobes of the corolla respectively of *L. chapmanii* are 11 mm and 4 mm long whereas those of *L. provincialis* are 6-7 and 3 mm long. Although the inner phyllaries of the heads of *L. chapmanii* are longer there is

filamentorum verus; lobi 3 mm longi. Achaenia 5 mm longa valde costata pilosa.

HOLOTYPE.—Franklin County, Florida: sand dunes along the Gulf of Mexico, Alligator Point, October 4, 1959, *Godfrey 58985* (deposited in the Gray Herbarium).

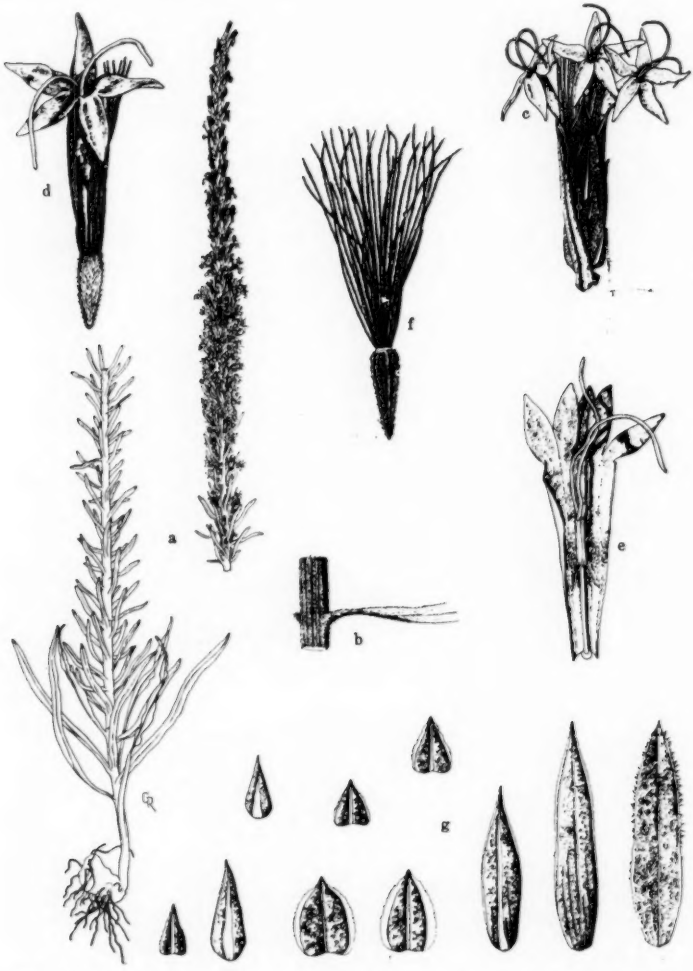


Fig. 2.—*Liatris chapmanii:* a, habit; b, small portion of stem with a leaf base; c, head; d, flower; e, portion of flower with corolla split longitudinally and spread open; f, achene; g, a representative series of phyllaries.

Observations on the Fleas (Siphonaptera) of Some Small Mammals in Northwestern Illinois

B. J. VERTS

Illinois Natural History Survey, Urbana

ABSTRACT: The relative infestation of small mammals by fleas was studied in northwestern Illinois. Eleven host species numbering 718 individuals were collected from February to October in 1958. Three hundred eighty-six fleas of 11 species were taken from these hosts. More fleas per host were collected in the cooler months than in the warmer months. *Orchopeas leucopus,* a flea often considered to infest *Peromyscus* without exhibiting an apparent preference as to species, may actually be more common on species which occupy woodland habitats. Mean numbers of fleas of each of three species on *Peromyscus leucopus,* a host species taken in all seasons, indicated that peak populations of the three species do not coincide.

A relatively large number of shrews and associated small mammals were trapped during a survey for rabies in shrews between February 14 and October 3, 1958. Fleas were removed from these specimens and submitted for identification to the Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey. Because relatively little is known about fleas in this section of the Midwest these records are believed to represent a contribution.

Acknowledgment.—These observations were supplementary to an investigation of sylvan rabies which was supported by a grant (No. E-1349) from the Division of Research Grants, U. S. Public Health Service, Department of Health, Education, and Welfare. Thanks are due Dr. C. O. Mohr for suggesting the study and for a critical reading of the manuscript and to Dr. L. J. Stannard for identifying the fleas. Also, Drs. T. G. Scott and R. E. Yeatter, and Mr. G. C. Sanderson gave help and advice which is gratefully acknowledged.

METHODS

Ninety-five trap lines, each consisting of 20 stations 10 yards apart with two break-back traps per station, were set along secondary road rights-of-way in Jo Daviess, Carroll, and Whiteside counties. The traps, baited with liver sausage to attract shrews, were allowed to remain in place for two consecutive nights. The traps were examined each morning, captured animals removed, and the bait replaced when necessary. Specimens obtained were placed in individual No. 1 paper bags.

In the laboratory, the contents of each bag were dumped into the center of a piece of brown wrapping paper. The sack was torn apart, and fleas clinging to the bag or to debris were collected with forceps and placed in a vial of 70 per cent alcohol. The mammal carcass was then brushed and combed thoroughly with the points of the forceps, and additional fleas clinging to the host were collected. Mammals which were badly deteriorated or partially eaten by other animals were not examined for fleas.

a variability in the shape of the outer ones of both plants, particularly as to the form of their tips and the width of the scarious margins, which makes them of little diagnostic value. Cilia on both the phyllaries and the bracts subtending the heads are more conspicuous and uniformly present in *L. provincialis* than in *L. chapmanii* but this is a matter of degree and cannot be satisfactorily expressed for purposes of distinction.

It may be argued *that L. provincialis* had better be treated infraspecifically with *L. chapmanii*. This, however, may be equally true with regard to certain others pairs of species of *Liatris*, for example, *L. secunda* and *L. pauciflora*, *L. tenuifolia* Nutt. and *L. laevigata*. It appears to me that the most recent revisionary treatment of *Liatris* by Gaiser (1946) is subject to considerable question as to the specific and infraspecific status accorded various taxa. Chromosome counts and chromosome morphology appear not to be very helpful within the Series in this genus as regards assigning status For instance, chromosome counts made by Gaiser (1950) for taxa in the Series Graminifoliae and Pauciflorae were n = 10 for all species and no karyotypic variation was observed which would be helpful in the question of status for the taxa. This is not to belittle Dr. Gaiser's work but suggests that if rank is to be ascertained other than by those criteria thus far employed, it must await investigations of a different kind.

Dr. Lloyd H. Shinners, Southern Methodist University, provided the Latin diagnosis. His generous aid is gratefully acknowledged. Illustrations were prepared by Mr. Grady W. Reinert. The details illustrated for each of the two species were drawn to the same scale.

REFERENCES

GAISER, L. O. 1946. The genus *Liatris*. *Rhodora*, **48**:165-183, 216-263, 273-326, 331-382, 393-412.

———. 1950. Chromosome numbers in *Liatris*. II. Graminifoliae and Pauciflorae. *Am. J. Bot.*, **37**:414-423.

TABLE I.—Numbers of each species of hosts examined for fleas and numbers of each species of fleas with which the hosts were infested in northwestern Illinois, February 14-October 3, 1958

Host Species	Number hosts examined	Species and Numbers of Fleas											Totals
		Orchopeas leucopus	*Epitedia wenmanni*	*Ctenophthalmus pseudagyrtes*	*Nearctopsylla genalis*	*Opisocrostis bruneri*	*Megabothris asio*	*Monopsyllus wagneri*	*Oropsylla arctomys*	*Corrodopsylla curvata*	*Stenoponia americana*	*Doratopsylla blarinae*	
Microtus pennsylvanicus	164	1	13	13			7	1	1	1			37
Microtus ochrogaster	69	1	5	11			2				2		21
Peromyscus maniculatus	115	8	10	6				16					40
Peromyscus leucopus	179	91	19	3				51					164
Blarina brevicauda	125		4	48	1		1	2		48		3	107
Reithrodontomys megalotis	15	2						1					3
Sorex cinereus	16			1									1
Mus musculus	19							3					3
Citellus tridecemlineatus	8					5							5
Zapus hudsonicus	6							2					2
Mustela rixosa	2		3										3
Totals	718	103	54	82	1	5	10	76	1	49	2	3	386

OBSERVATIONS

Of 790 hosts captured, 718 were examined for fleas. Three hundred eighty-six fleas, representing 11 species, were collected. The species and numbers of hosts and fleas are shown in Table I.

Orchopeas leucopus (Baker) was the most numerous of the fleas collected; 103 were taken. Although five species of hosts were infested, 99 of the specimens were obtained from *Peromyscus*. In New York, Benton and Cerwonka (1960:389) collected this species with about equal frequency from *Peromyscus leucopus* (Rafinesque) and *Peromyscus maniculatus* (Wagner). In northwestern Illinois, more than seven times the number of *O. leucopus* per host were taken from *P. leucopus* than from *P. maniculatus*. In this area, *P. maniculatus* is represented by the form *Peromyscus maniculatus bairdii* (Hoy and Kennicott) which inhabits grassland and open fields, and tends to be ecologically separated from *P. leucopus* in most habitats. In New York, *P. maniculatus* is most often represented by the form *Peromyscus maniculatus gracilis* (Le Conte) which is an ecological associate of *P. leucopus* (Hamilton 1943:271). It may be that woodland is a more suitable habitat for this species of flea, and *P. maniculatus* is commonly infested only where the habitat is such that it is closely associated with *P. leucopus*. Mohr (1956:390) believed that suitability of habitat to chiggers (Acarina) in New Guinea was more important in determining the rates of infestation per host than was preference exhibited by the ectoparasites for a specific host. Layne (1958:6) listed *O. leucopus* from *P. leucopus* and *P. maniculatus* taken on strip-mined land (at Pyatt) in southern Illinois where in many situations these hosts are closely associated (Verts 1957:56).

The mean number of *O. leucopus* on *P. leucopus* was 0.2 or fewer per individual in February and April but reached a peak of 2.0 per individual in May. The mean number per specimen declined to the previous level in the summer months (June-August) but increased to about 0.6 per host in October (Fig. 1).

Ctenophthalmus pseudagyrtes Baker was the second most common species of flea collected. Six species of mammals were infested (Table I). More than half of the specimens were collected from short-tailed shrews, *Blarina brevicauda* (Say), and more than twice as many fleas per specimen were obtained from this host as from any other. Benton and Cerwonka (1960:388) consider this species of flea to be one of the less host specific. From February to June, when 15 or more *Blarina* were examined per month, the mean number of *C. pseudagyrtes* per individual fluctuated between 0.2 and 0.5. The rate of infestation tended to be greater in the warmer months. To few *Blarina* were captured in the other months to obtain comparable data.

Monopsyllus wagneri (Baker) was the next most commonly collected flea. Seventy-six specimens were obtained from seven species of mammals (Table I). More than 88 per cent of the specimens were taken from *Peromyscus*, but about twice as many per host were found

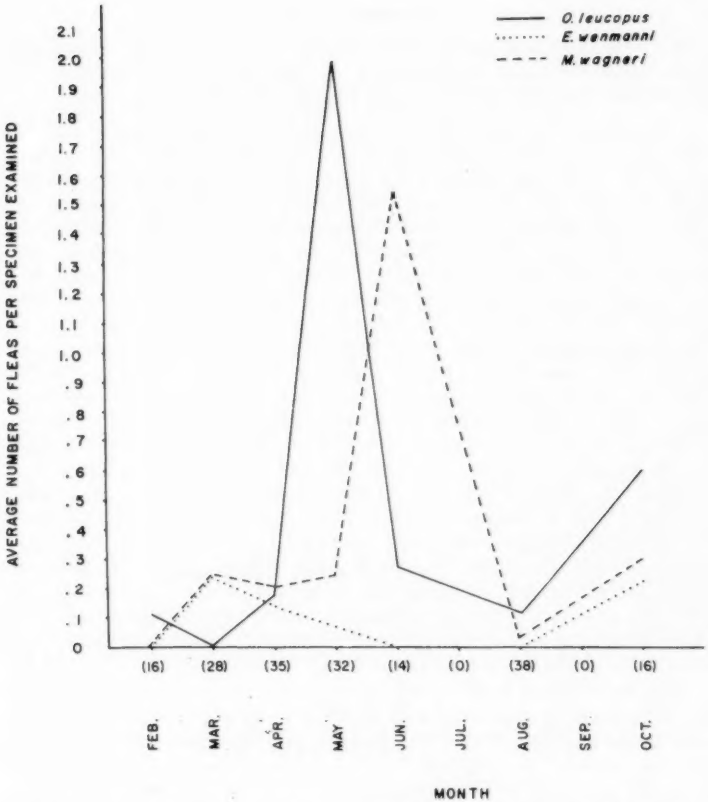


Fig. 1.—Mean numbers of three species of fleas collected from *Peromyscus leucopus* each month, February-October, 1958. (Numbers in parentheses indicate numbers of hosts examined.)

on *P. leucopus* as on *P. maniculatus*. On *P. leucopus*, the mean number of this species per host was about 0.3 in March, April, and May (Fig. 1). In June, when 14 *P. leucopus* were examined, 1.6 fleas per host were collected. Only 0.03 per host were collected from 38 specimens examined in August, but there was an increase to slightly above the pre-June level of infestation in October. More *M. wagneri* were also collected from *P. maniculatus* in June than in other months.

Epitedia wenmanni (Rothschild) was collected from six species of mammals (Table I). Fifty-four specimens were taken, 29 from *Peromyscus*. The mean number per host was nearly equal on *P.*

leucopus and *P. maniculatus* (about 0.1); the rate of infestation was slightly less on *Microtus pennsylvanicus* (Ord) and *Microtus ochrogaster* (Wagner). On *P. leucopus,* from which about one-third of these fleas were obtained, a mean of 0.3 per host was collected in March. There was a gradual decline in mean numbers per host in April and May; none was taken in the summer months. The mean number per *P. leucopus* in October was the same as that in March. Although fewer were collected from *P. maniculatus,* a similar seasonal trend in the rate of infestation was evident.

Corrodopsylla curvata (Rothschild) was found only on *B. brevicauda* and *M. pennsylvanicus;* 48 were collected from the former, 1 from the latter. Holland (1949:95) reported that this species was often associated with *Sorex.* The 16 *Sorex cinereus* Kerr examined were not infested (Table I). No *C. curvata* were collected from *Blarina* in February and March. From April to June there was an increase from 0.4 to 0.7 per specimen. Although this flea was collected from *Blarina* in July, August, and October, too few hosts were examined to provide comparable data.

Of the remaining six species of fleas infesting the small mammals, 10 or fewer of each were collected (Table I). *Opisocrostis bruneri* (Baker) and *Doratopsylla blarinae* C. Fox, host specific for *Citellus* (Jellison 1947:64) and *Blarina* (Benton and Cerwonka 1960:389), respectively, were taken only from their respective hosts. One *M. pennsylvanicus* bore a single *Oropsylla arctomys* (Baker), a flea which is usually associated with woodchucks, *Marmota monax* (Linnaeus), (Benton and Cerwonka 1960:389). *Megabothris asio* (Baker) and *Stenoponia americana* (Baker) were also found on *Microtus;* a single specimen of the former flea was taken from *Blarina.* A single *Nearctopsylla genalis* (Baker) was taken from *Blarina.*

DISCUSSION

The relatively large numbers of different species of fleas collected from *Blarina* (7) and *Microtus* (8) are probably a reflection of the habits of the two species. Tunnels constructed by *Microtus* are extensively used by *Blarina* and other small mammals, which affords ample opportunity for exchange of fleas between host species. Fleas which occurred in relatively large numbers on *Microtus* (*Megabothris asio*) and *Blarina* (*Ctenophthalmus pseudagyrtes* and *Corrodopsylla curvata*) were occasionally interchanged (Table I).

Adequate numbers of *P. leucopus* were taken in all seasons to permit comparison of relative abundance of three species of fleas with which they were infested. There appears to be a seasonal difference in the rates of infestation by these fleas. *E. wenmanni* was more common in March and October, but less so in spring and summer; *O. leucopus* was more than three times as abundant in May as in any other month; *M. wagneri* was nearly four times as abundant in June as in any other month (Fig. 1).

The small number of fleas of all species collected from *P. leucopus* in August, when more were examined and the rate of capture per unit effort was the highest, may be a result of fleas leaving the dead hosts after the carcasses had begun to cool. This may be less likely in winter when the insect parasites would tend to be immobilized by cold.

The mean number of all species of fleas infesting all species of mammals increased from February to June. Although fewer mammals were examined in July, August, and October than in other months, there appeared to be a decline in mean numbers per host in the warmer months followed by a slight increase in October.

REFERENCES

BENTON, A. H. AND R. H. CERWONKA 1960. Host relationships of some eastern Siphonaptera. *Am. Midl. Nat.*, **63**(2):383-391.

HAMILTON, W. J., JR. 1943. The mammals of eastern United States. Comstock Publishing Company, Inc., Ithaca, N. Y. 432 p.

HOLLAND, G. P. 1949. The Siphonaptera of Canada. Dominion of Canada Dept. of Agr. Tech. Bull. 70. 306 p.

JELLISON, W. L. 1947. Siphonaptera: host distribution of the genus *Opisocrostis* Jordan. *Am. Microscop. Soc. Trans.*, **66**(1):64-69.

LAYNE, J. N. 1958. Records of fleas (Siphonaptera) from Illinois mammals. *Chicago Acad. Sci., Nat. Hist. Misc.*, **162**:1-7.

MOHR, C. O. 1956. Comparative infestations by ectoparasites of two native rats of Sansapor, New Guinea. *Am. Midl. Nat.*, **55**(2):382-392.

VERTS, B. J. 1957. The population and distribution of two species of *Peromyscus* on some Illinois strip-mined land. *J. Mammal.*, **38**(1):53-59.

Wintering Distribution Changes in Mallards and Black Ducks

PAUL A. JOHNSGARD

Department of Zoology, University of Nebraska, Lincoln

ABSTRACT: Through the use of data compiled by the Audubon Society's annual Christmas Counts, an attempt has been made to trace the distributional changes of wintering Mallards and Black Ducks in the eastern states from 1900 to the present. During this period the Black Duck has increased relative to the Mallard in few if any states (the Great Lakes region), whereas the Mallard has increased nearly everywhere else (except in the extreme northeast), particularly in the southern coastal states. Deforestation and changes in land use are suggested as probable reasons for this trend, which is not likely to be reversed.

Although several rather spectacular shifts in the distributions of various American species of birds have become evident in recent years, the "colonization" of the eastern states by the Mallard (*Anas platyrhynchos*) has not been so generally recognized. The magnitude of this range extension has been great nevertheless, and the probable reasons for it have been discussed elsewhere (Johnsgard, 1959, 1961). Concomitant with the increase of the Mallard in the eastern states, the native Black Duck (*Anas rubripes*) has suffered a decline in numbers, and apparently for some of the same reasons as the Mallard has increased. Since this trend is not likely to be reversed in the future, it will be of interest to follow it carefully and thus possibly to predict the fate of the Black Duck.

Wing (1943) became interested in the ratios of Mallards to Black Ducks throughout the eastern states before the range shift was at all apparent, and calculated state ratios for the two forms on the basis of the data provided by the annual Audubon Society Christmas counts for the forty years 1900 to 1939. He found that the average ratios for that period (which, because of the continuously increasing number of counts, is probably typical of the situation somewhat after the midpoint of 1920) indicated that the zone of equal ratios fell in a north-south line between Michigan and western Florida. East of this line the Black Duck was markedly dominant over the Mallard and west of it the Mallard was equally dominant. Wing's data are presented in Table I, but they are converted from simple Mallard: Black Duck ratios to the alternative method of calculating the relative percentages of each form in the combined sample. This latter means of presenting ratio data has certain statistical advantages (Hickey, 1957). Arguments supporting the use of these data as unbiased estimates of wintering Mallard and Black Duck populations have been presented elsewhere (Johnsgard, 1959), and so will not be repeated here.

To test the possibility that these counts might indicate the degree to which the Mallard has moved eastward in recent years, it was de-

cided to bring these calculations up to date, by collating the Christmas Count records for the twenty years 1940 to 1959. Since the numbers of counts and counters has increased enormously since 1940, the data were divided into earlier (1940-1949) and later (1950-1959) periods. Again, although the averages for these total periods are presented (Table I), they probably reflect the existing conditions somewhat after the mid-points of the periods. It must be remembered too that changes in the ratios can be attributed both to Mallard increases in the East and to Black Duck decreases, rather than only to Mallard increases alone.

The data for the years 1940 to 1949 show some interesting differences from Wing's data for the preceding forty years. Of the states east of the Michigan to western Florida zone, one state (Florida) exhibits a majority of Mallards in the wintering population. Fourteen states exhibit what are probably significant reductions in the percentages of Black Ducks, with the most marked changes occurring in Florida, North Carolina, and Michigan. Only four states (Wisconsin, Kentucky, West Virginia and Virginia) exhibit noticeable increases in Black Duck ratios; of these West Virginia's data are probably not based on a sufficient sample. Since Wing's (1943) data did not include information on sample size it is impossible to evaluate these differences statistically.

The data for the years 1950 to 1959 bring to light some even more striking changes. Five states (Florida, Georgia, South Carolina, North Carolina and Ohio) east of the Michigan-western Florida zone exhibit majorities of Mallards in the samples. Eighteen states exhibit marked declines in Black Duck ratios from those presented by Wing. Only two states (Minnesota and Wisconsin) exhibit significant increases in Black Duck ratios over those of preceding years.

To provide a relatively up-to-date picture of the situation, data for the years 1958 to 1960 are also presented in Table I. Although in some cases the sample sizes are too small to be useful, in most a still greater decrease in Black Duck ratios is evident. It is astonishing to contemplate that in twenty years Delaware, for example, has undergone a shift in ratios from an almost pure Black Duck population to one in which Mallards are more abundant than Black Ducks. Other only slightly less remarkable examples are provided by the coastal states from North Carolina to Florida. On the other hand, the northern interior states have undergone less pronounced decreases, such as, for example, Michigan, Illinois, Indiana and Ohio. If a line delineating the zone of equality between Mallard and Black ratios were to be drawn today, it would still have to pass through Michigan at the north, but be deflected eastward to the south so as to pass through Virginia and North Carolina. Only in Maine and the Canadian maritime provinces may the wintering population still be considered "pure" Black Duck. It appears, therefore, that the Mallard has been invading the East by a "flanking" movement along the Gulf Coast states. It is hard to determine how rapidly the Mallard has colonized

TABLE I.—Relative numbers of wintering Mallards and Black Ducks, based on Audubon Christmas Counts from 1900-1960

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
Nova Scotia			
1950-1959	5,962	2	99.97
1958-1960	1,865	1	99.95
Quebec			
1940-1949	2,092	81	96.27
1950-1959	6,314	155	97.60
1958-1960	1,821	50	97.33
Ontario			
1900-1939	.....	.....	97.51
1940-1949	9,370	1,450	86.59
1950-1959	15,163	7,936	65.36
1958-1960	7,261	3,793	65.69
Maine			
1940-1949	1,773	2	99.89
1950-1959	6,543	43	99.35
1958-1960	5,102	29	99.43
New Hampshire			
1950-1959	5,791	171	97.13
1958-1960	1,736	234	88.12
Vermont			
1940-1949	272	11	96.11
1950-1959	538	12	97.82
1958-1960	170	5	97.14
Massachusetts			
1900-1939	.....	.....	99.28
1940-1949	78,570	472	98.52
1950-1959	117,499	7,002	94.37
1958-1960	53,679	4,606	90.38
Rhode Island			
1900-1939	.....	.....	99.35
1940-1949	18,468	101	99.45
1950-1959	18,759	410	97.86
1958-1960	6,800	221	96.85
Connecticut			
1900-1939	.....	.....	94.31
1940-1949	19,398	577	97.11
1950-1959	39,802	13,646	74.47
1958-1960	15,269	8,838	63.34
New York (entire state)			
1900-1939	.....	.....	96.12
1940-1949	135,376	13,426	90.97
1950-1959	202,713	30,563	86.90
1958-1960	65,891	14,417	82.05

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
New York (Long Island)			
1940-1949	78,172	4,990	94.00
1950-1959	125,489	13,711	90.15
1958-1960	43,530	7,276	85.68
New York (rest of state)			
1940-1949	57,204	8,436	87.15
1950-1959	77,224	16,852	82.09
1958-1960	22,361	7,141	75.79
New Jersey			
1900-1939	.....	.....	99.17
1940-1949	50,305	3,922	92.76
1950-1959	226,744	28,631	88.79
1958-1960	104,640	10,542	90.85
Pennsylvania			
1900-1939	.....	.....	95.39
1940-1949	63,933	9,953	86.52
1950-1959	90,307	55,738	61.83
1958-1960	20,456	21,043	49.29
Delaware			
1900-1939	.....	.....	99.08
1940-1949	21,777	634	97.17
1950-1959	118,489	85,175	58.18
1958-1960	31,288	42,432	42.44
Maryland			
1900-1939	.....	.....	94.08
1940-1949	23,309	3,108	88.23
1950-1959	102,184	60,343	62.87
1958-1960	43,482	30,719	58.60
Washington, D.C.			
1940-1949	1,854	376	83.14
1950-1959	7,619	2,170	77.83
1958-1960	1,717	449	79.27
Virginia			
1900-1939	.....	.....	67.53
1940-1949	15,557	2,599	85.67
1950-1959	68,736	31,259	68.74
1958-1960	26,531	13,706	65.94
North Carolina			
1900-1939	.....	.....	90.13
1940-1949	3,133	1,831	63.10
1950-1959	28,830	29,522	49.41
1958-1960	16,849	16,593	50.38

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
South Carolina			
1900-1939	.....	.....	71.35
1940-1949	3,232	1,534	67.84
1950-1959	3,169	49,281	6.04
1958-1960	1,483	32,341	4.59
Georgia			
1900-1939	.....	.....	70.58
1940-1949	21,266	10,882	66.10
1950-1959	169	2,258	6.96
1958-1960	210	984	17.59
Florida			
1900-1939	.....	.....	65.98
1940-1949	1,188	1,854	29.09
1950-1959	1,142	4,164	21.52
1958-1960	304	1,296	19.00
Ohio			
1900-1939	.....	.....	66.89
1940-1949	33,983	22,266	60.32
1950-1959	105,670	150,582	41.23
1958-1960	65,153	78,541	45.34
West Virginia			
1900-1939	.....	.....	88.01
1940-1949	622	35	94.67
1950-1959	1,321	674	66.21
1958-1960	642	427	60.06
Kentucky			
1900-1939	.....	.....	15.31
1940-1949	8,216	11,083	42.74
1950-1959	39,902	375,891	9.60
1958-1960	6,912	23,875	22.45
Tennessee			
1900-1939	.....	.....	19.54
1940-1949	4,477	33,844	11.68
1950-1959	6,044	354,969	1.67
1958-1960	8,288	176,772	4.48
Alabama			
1940-1949	4,257	19,380	18.02
1950-1959	5,024	59,720	7.70
1958-1960	89	380	18.98
Mississippi			
1900-1939	.....	.....	14.56
1940-1949	96	1,119	7.90
1950-1959	2	11,621	0.02
1958-1960	0	178	0.00

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
Michigan			
1900-1939	.....	.....	71.75
1940-1949	7,800	6,656	53.91
1950-1959	15,275	11,990	56.02
1958-1960	2,146	1,868	53.46
Indiana			
1900-1939	.....	.....	21.37
1940-1949	26,425	93,660	22.03
1950-1959	68,372	1,442,230	4.53
1958-1960	4,935	69,187	6.65
Illinois			
1900-1939	.....	.....	8.52
1940-1949	51,625	2,311,226	2.19
1950-1959	74,486	1,410,753	5.01
1958-1960	11,112	290,805	3.68
Wisconsin			
1900-1939	.....	.....	10.10
1940-1949	7,175	14,794	32.38
1950-1959	12,543	41,853	23.06
1958-1960	3,452	22,118	13.50
Minnesota			
1900-1939	.....	.....	0.07
1940-1949	36	3,337	1.07
1950-1959	682	8,705	7.26
1958-1960	31	4,463	0.69
Iowa			
1900-1939	.....	.....	0.22
1940-1949	65	29,745	0.22
1950-1959	210	45,724	0.46
1958-1960	207	13,949	1.46
Missouri			
1900-1939	.....	.....	0.70
1940-1949	460	94,516	0.48
1950-1959	163	275,485	0.06
1958-1960	93	168,045	0.06
Arkansas			
1900-1939	.....	.....	0.33
1940-1949	1	871	0.12
1950-1959	136	479,094	0.03
1958-1960	32	156,625	0.02
Louisiana			
1900-1939	.....	.....	7.57
1940-1949	490	20,626	2.33
1950-1959	194	28,228	0.68
1958-1960	54	4,581	1.16

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
North Dakota			
1940-1949	1	1,977	0.05
1950-1959	0	1,661	0.00
1958-1960	0	99	0.00
South Dakota			
1900-1939	.....	.....	0.21
1940-1949	10	340,265	0.003
1950-1959	35	484,132	0.01
1958-1960	10	300,664	0.003
Nebraska			
1940-1949	0	475	0.00
1950-1959	0	119,635	0.00
1958-1960	0	226,468	0.00
Kansas			
1940-1949	13	18,457	0.07
1950-1959	23	278,104	0.01
1958-1960	4	58,712	0.007
Oklahoma			
1940-1949	65	271,791	0.02
1950-1959	42	219,765	0.02
1958-1960	5	34,058	0.01
Texas			
1900-1939	.....	.....	0.85
1940-1949	29	371,396	0.01
1950-1959	122	780,629	0.01
1958-1960	17	134,715	0.01

the eastern states as a breeding bird, but counts made by federal and state biologists during the breeding season indicate that Mallard-Black Duck ratios in the northern states and provinces during the period 1948-1956 closely parallel the wintering ratios of those areas for the same period (Johnsgard, 1959).

It would appear that the Mallard has in the past few decades made enormous inroads into what formerly was predominantly Black Duck territory, whereas the reverse is true only to a very limited extent in the Great Lakes region. Probably this can be attributed to the great changes in land use, and the deforestation, which have occurred in the East during the present century, and which have had the effect of decreasing Black Duck breeding habitat while at the same time increasing Mallard habitat. Whether sufficient preservation and regeneration of the northeastern forests will occur to permit the Black Duck to retain a stronghold is impossible to predict, but it appears likely that the Black Duck, through hybridization with the much larger

Mallard gene pool and through the constant reduction of its breeding habitat, may eventually disappear as a distinct entity from our fauna.

Acknowledgment.—This study was done at Cornell University under the support of fellowships from the Cornell University Graduate School and the National Science Foundation. I would like to express my appreciation to these agencies as well as to Dr. C. G. Sibley, my graduate committee chairman.

REFERENCES

HICKEY, J. J. 1957. Editorial note. *J. Wildl. Mgmt.*, **21**:347.

JOHNSGARD, P. A. 1959. Evolutionary relationships among the North American mallards. Ph.D. Thesis, Cornell University. 153 p.

———1961. Evolutionary relationships among the North American mallards. *Auk*, **78**:3-43.

WING, L. 1943. Relative distribution of Mallard and Black Duck in winter. *Ibid.*, **60**:438-439.

The Effects of Fires in the Okefenokee Swamp in 1954 and 1955

EUGENE CYPERT

U. S. Fish and Wildlife Service, Waycross, Georgia

ABSTRACT: In 1954 and 1955 during an extended drought, serious fires occurred in the Okefenokee Swamp and on the adjacent upland. There was considerable destruction of pine timber on the upland and some damage to the cypress and blackgum forests within the swamp but the belief that the whole character of the swamp has been altered is erroneous.

Recurrent droughts and fires have long played an important part in the ecology of the swamp as is evidenced by charred stumps embedded in the peat and by charcoal deposits several feet below the surface.

Five major fires between July 1954 and June 1955 burned over about 318,000 acres of the swamp and 140,000 acres of adjacent upland. Most of the swamp was lightly or moderately burned. Severe burns were spotty. Coppice growth is rapidly replacing the timber which was killed in the more severely burned areas. The numbers of otters, raccoons, snakes and most fish were drastically reduced during the drought. Alligators, sandhill cranes, herons, waterfowl and bears were not adversely affected and some of these may have actually been favored.

INTRODUCTION

In 1954 and 1955, during an extended drought, fires occurred in the Okefenokee Swamp and surrounding upland in southeast Georgia and northeast Florida. The drought was so severe that the upper layer of the peaty floor of the swamp dried out and became flammable. The peat fires which ensued could not be controlled, with the result that the fire swept over about 80 per cent of the Swamp. Also, about 140,000 acres of pine forests surrounding the swamp were so severely burned that an almost complete kill of timber followed.

Because of the destruction in the large area of surrounding pine lands and because of severe burns in certain places within the Okefenokee Swamp, a misunderstanding about the effects of the fire on the character of the swamp has become prevalent. It has been generally believed that the fires have destroyed the swamp's cypress and blackgum forests, leaving charred desolation nearly void of life.

Actually, while some parts of the swamp were severely burned, most of the area reached by fires was only moderately or lightly burned and only temporary alteration, or none at all, resulted.

This paper is an attempt to appraise the effects of the drought and the fires on the ecology of the swamp.

DESCRIPTION OF THE SWAMP

Okefenokee Swamp covers approximately 412,000 acres in Ware, Charlton and Clinch counties, Georgia, and Baker County, Florida.

Approximately 321,725 acres of the swamp and 9,250 acres of adjacent upland are included in the Okefenokee National Wildlife Refuge.

The elevation above sea level ranges from about 130 feet on the northeast side to about 105 feet on the southwest side. The swamp's existence is due to Trail Ridge, a sand bar formed during the early Pleistocene period when the coast line was about 70 miles farther inland and the sea level was about 160 feet higher in relation to the land than at present. After the recession of the coast line, this ridge acted as a barrier to prevent the drainage of the shallow basin thus formed (MacNeil, 1940).

The principal outlet of the swamp is the Suwannee River which empties into the Gulf of Mexico. Some of the drainage is through the St. Mary's River which empties into the Atlantic Ocean.

Considering the size of the swamp, the watershed of the Okefenokee is small. Along the east and northeast sides the drainage area, which extends from the crest of Trail Ridge to the swamp edge, averages only about one mile in width. The sandy soil of Trail Ridge erodes very little and, consequently, deposits little silt into the swamp. On the north and northwest sides, about 300,000 acres drain into the swamp. This is flat, sandy land, with very little, if any, erosion. The almost complete absence of siltation accounts for the Okefenokee's persistence.

Except for a few small open water areas, the Okefenokee basin is filled with peat almost to the average water level. This peat deposit, which varies up to 20 feet or more in depth, serves as the floor of the swamp. About 85 per cent of the swamp is covered, more or less densely, with forests in which either pond cypress (*Taxodium distichum nutans*) or swamp blackgum (*Nyssa sylvatica biflora*) predominate. The principal secondary species are red bay (*Gordonia lasianthus*), white bay (*Magnolia virginiana*), sweet bay (*Persea borbonia*), red maple (*Acer rubrum*), cassena (*Ilex cassine*) and titi (*Cyrilla racemiflora*).

The forest understory is principally hurrah bush (*Desmothamnus lucidus*), titi, swamp fetterbush (*Leucothoe racemosa*), he-huckleberry (*Arsenococcus ligustrinus*), poor-man's soap (*Clethra alnifolia*), black bamboo (*Smilax laurifolia*), red bamboo (*Smilax walteri*), and sweet spire (*Itea virginica*).

The so-called "prairies," which are actually marsh and open water areas, cover the remainder of the swamp. These prairies contain a variety of herbaceous marsh and aquatic vegetation. White water lilies (*Nymphaea adorata*), spatterdock (*Nuphar* advena), beakrush (*Rhynchospora inundata*), neverwet (*Orontium aquaticum*), chain fern (*Woodwardia virginica*), paintroot (*Gyrotheca tinctoria*), maidencane (*Panicum hemitomon*), pipewort (*Ericaulon compressum*) and false maidencane (*Sacciolepis striata*) are prominent.

Scattered throughout the prairies are small clumps of trees and shrubs called "houses." These houses vary in size from only a few

milacres to several acres. Their composition is usually about the same as that of the forested areas. Larger stands of timber within the swamp are called "bays."

HISTORY OF FIRES IN OKEFENOKEE SWAMP

It is evident that fires have long played an important part in the ecology of Okefenokee Swamp. We have records of droughts and accompanying fires in 1844, 1860, 1910 and 1932.

John M. Hopkins (1947) quotes Owen K. Mizell, an early resident of the Okefenokee country, as saying, "in 1844 there was a terrible drought and the Okefenokee caught fire and holes were

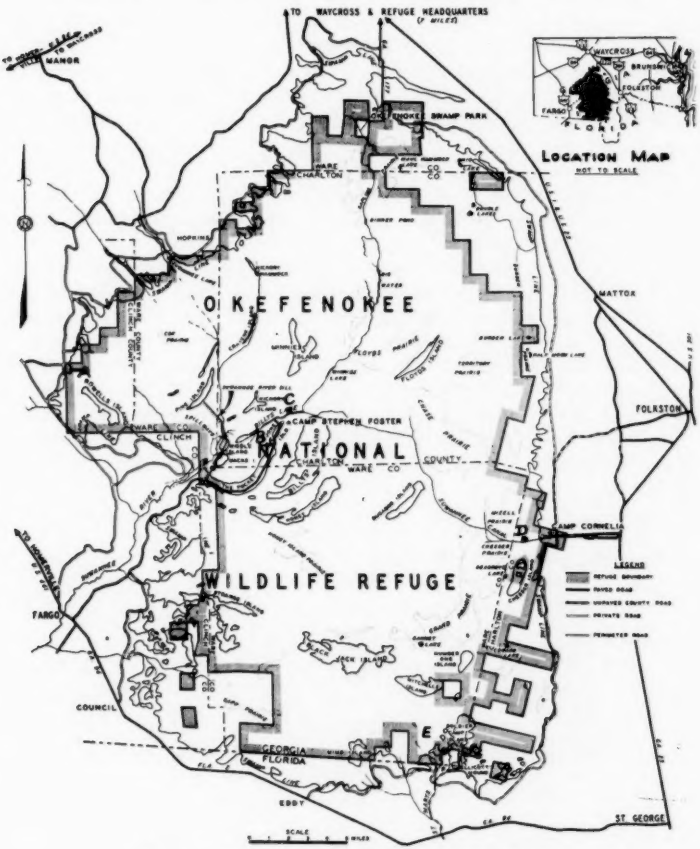


Fig. 1.—Okefenokee National Wildlife Refuge.

burned out which were the cause of the majority of the lakes in there."

The Okefenokee prairies were caused by extremely hot fires which killed all plants, root systems included, and burned away the peat to a low enough level to prevent the re-establishment of woody vegetation. Charred stumps, embedded in the peat throughout the prairies, are evidence of extensive forests which were killed by fire.

Fires which resulted in prairie formation must have occurred during droughts which were much more extreme than any in recent years. Undoubtedly, the prairie lakes were the results of great pockets being burned out in the peat. There are at least 40 of these lakes large enough to be designated by names and innumerable small un-named "gator holes." The largest are Gannett Lake (28 acres), Coward Lake (22 acres) and Double Lakes (36 and 18 acres).

In order to learn whether the lakes exist because of the topography of the underlying sand floor of the swamp or because of the topography of the overlying peat, series of soundings were run across three of them: Buzzard Roost, Monkey and Cooter Lakes. In no case was there an indication of a relationship between the presence of the lake and the topography of the underlying sand floor. In other words, the lakes are holes in the peat, rather than holes in the underlying sand, which gives credence to the belief that the lakes were fire caused.

While the fire of 1844 may have been severe enough to have caused prairies and lakes, we know that there were extensive prairies in Okefenokee Swamp antecedent to that fire. General Charles Flőyd, who entered the swamp with a company of men during the Seminole Wars in 1838, wrote of a large lake east of Floyd's Island (Hopkins, 1947). This "lake" must have been Chase Prairie. He also wrote of an extensive prairie west of Floyd's Island "level as a lake and covered with short grass and adorned with beautiful islands" (Walker and King, 1947). This area is known as Floyd's Prairie.

There is evidence that extremely severe fires occurred in the

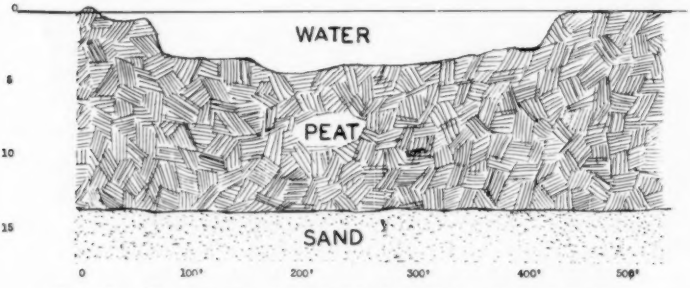


Fig. 2.—The topography of Monkey Lake indicating the relation between surface peat and sand floor.

Okefenokee much earlier than those which caused the present prairies. J. Gordon Erdman made a series of corings in the peat in Floyd's Prairie, Chase Prairie and near Minnie's Lake in 1957. Charcoal was found at depths of 5′3″ and 5′9″ in one coring and at 4′5″, 6′7″ and 7′3″ in another. This last coring was made to a depth of 7′7″ which was the deepest made by Dr. Erdman (correspondence).[1]

Datings have not been made of these corings at this writing. Some idea of the rate of peat accumulation may be obtained from information submitted by Dr. Erdman on the datings of samples collected at a depth of 3′10″ to 4′3″ in Tamarack Swamp near Columbus, Pennsylvania and 3′7″ to 3′11″ in Graveline Bay, near Pascagoula, Mississippi. By C^{14} datings, the former was given an age of 2820 ± 250 years, the latter 2220 ± 180 years.

Since the Okefenokee corings indicate that the peat has been burned away to depths of several feet on several occasions and then redeposited, it can be assumed that the deeper charcoal deposits were the results of fires which occurred many thousands of years ago.

FIRES DURING THE 1954-1955 DROUGHT

During the period from January 1, 1954 to June 30, 1955, only 44.25 inches of rainfall were recorded at the Weather Bureau station at Camp Cornelia on the east side of Okefenokee Swamp. During the entire year 1954 there were only 26.07 inches of precipitation which is in sharp contrast to the average annual precipitation of 56.39 inches from 1939 to 1953.

The water level at Camp Cornelia fell to a low of 117.56 on November 14, 1954. This was 3.53 feet below the 1941-53 average water level at this station. By November 22, the water level at Billy's Lake had fallen to 110.44 feet, 3.92 feet below the 1941-53 average. The bed in the upper part of Billy's Lake went dry, as did much of Minnie's Lake and Big Water Lake. At this time there was very little surface water anywhere in the swamp.

During such extreme drought, the upper part of the swamp's peat bed dries out and the entire surface of the swamp's floor becomes tinder. If fire enters the swamp at such a time, there is no known way to control it.

Roy Moore (1955) described two types of swamp fire:

> "One being the surface fire that often moves fast, burning combustible materials on and above the swamp floor, and including crown fires that flame through the tree tops. Surface fires usually succumb to a heavy shower of rain. The other type is the peat fire that burns below the surface in the organic soil and debris of the swamp floor. Peat fires may be started by lightning or by surface fires. They move slowly in an irregular patchwork pattern. Sometimes they

[1] These data furnished by J. G. Erdman, Mellon Institute, Multiple Fellowship on petroleum sponsored by Gulf Research and Development Company.

> go out for no apparent cause; and often they continue to burn through half a foot or more of rain, until with the return of dry windy weather, they may give rise to the fast moving surface fires. A peat fire destroys every living thing that can't get out of its way. The roots of a giant cypress are burned away as readily as those of a hurrah bush."

A fire sweeping across the swamp may gain such headway that control, when it reaches the upland, is extremely difficult.

Billy's Island Fire.—The first major fire of the 1954-1955 drought occurred on Billy's Island. This fire, which was probably caused by lightning, burned from July 6 to July 12, 1954 and swept over the whole of Billy's Island, which is about 3000 acres in size. Probably the peat was not dry enough at this time to burn. The fire did not extend beyond the limits of the island.

Very few trees were killed. The accumulation of litter burned fairly clean and this proved later to be the salvation of the timber on the island. When it burned over again the following March, the fire was not nearly as severe as it might have been had the July fire not occurred.

Mule-tail Fire.—The "Mule-tail Fire" began on November 27, 1954. It has been told that this fire was started by a mule which was being used by Negro laborers collecting turpentine gum in the pine woods just southeast of the refuge. It is said that the mule switched its tail into a barrel of turpentine gum, then switched it into a fire which the laborers were warming by, then, its tail a torch, raced through the woods, scattering fire as it went. The account is probably apocryphal but it is a good story and has been widely circulated. At any rate, the fire was started by turpentine collectors.

The first control efforts were made toward preventing the spread of the fire through the upland. The swamp was regarded as a fire break. But it was dry enough that the fire swept westward into the swamp and then northward on a five mile front. Re-emerging on the upland on the east side of the swamp near Chesser Island, the fire crowned in the pine woods causing an almost complete kill on 20,650 acres of timber. An estimated 33,350 acres of swamp burned over. The fire was brought to a stop by a shower the night of December 5.

The Big Fire.—The most extensive fire of the drought period had two separate origins. One, which was probably the result of lightning, was discovered October 6, 1954. This fire began on the west side of the swamp about one mile northeast of Rowell's Island. It burned slowly and smouldered along for the next five months.

The other fire, which was discovered March 5, 1955, was of incendiary origin. It resulted from the setting of several fires along a seven mile stretch between Turkey Branch and Suwannee Creek from one to three miles west of the refuge.

These two fires came together on or about March 9 and continued to burn and spread until May 14, when stopped by rain.

Approximately 318,000 acres of swamp burned over. About 11,100 acres of pine timber on the upland were destroyed before the fire was brought under control.

Besides burning over approximately 279,000 acres of swamp which had not previously been burned during the drought, this fire reburned all of the 39,000 acres of swamp which had been burned in the other fires.

The State Forest Fire.—A fire of incendiary origin began near the north end of the swamp on Waycross State Forest March 6, 1955. This fire severely burned pine lands on the upland causing an almost complete kill of timber on about 22,500 acres. About 5,000 acres of swamp were burned over. It was brought under control March 14.

St. Regis Fire.—The most destructive fire of the drought was set by lightning at a point about nine miles northwest of Fargo, June 8, 1955, and spread rapidly eastward causing almost complete kill of pine timber on about 82,500 acres, mostly on lands of St. Regis Paper Company. This fire was brought under control at the swamp's edge near the Suwannee River and at about the limits of the March burn.

GENERAL EFFECTS OF THE FIRE ON THE ECOLOGY OF THE SWAMP

As stated above, the effect of the fires within the swamp was not as destructive nor as enduring as has been supposed by many who have seen only the severe destruction of the pine timber adjacent to the swamp. It was only where pockets of peat were burned out

Fig. 3.—Invasion of a severely burned spot near Soldier Camp Island by woody and herbaceous vegetation three years after the 1954-55 fires.

that the larger cypresses and blackgums were killed. These were encountered only occasionally. Where only surface fires occurred, the larger trees survived.

The fires in the cypress and blackgum bays burned with varying degrees of severity. In places there were pockets of peat burned out sometimes to a depth of two or three feet. Usually all trees were killed where peat burned to this depth. These pockets were usually less than 1/10 acre. Over most of the area the burns were surface fires which generally killed most of the reproduction and underbrush but rarely burned severely enough to kill the larger trees. In many places the fire swept over lightly, burning the surface duff and killing only the smaller underbrush. Some places were missed entirely. At no place was the fire intense enough to cause a complete kill of woody cover over as much as one acre.

The most severe burns occurred in places where timber operations had been conducted in past years, probably because the hottest fires occurred where low brushy growth was most dense, as in places where trees had been cut and skidded. Virgin cypress forest usually burned lightly and sustained little damage; virgin forest in which blackgum and bay were predominant usually burned lightly except that there were occasional severely burned small pockets.

In order to arrive at an estimate of the extent and damage in parts of the swamp where the damage was considered typical, two transects of 50 chains each were staked out. One of these extended from the upland at a point about one mile northeast of the north tip of Rowell's Island and ran eastward into the swamp (Fig. 1, A). The other extended from the Pocket near Jones Island westward and northward into the swamp (Fig. 1, B). Both of these transects were through typical blackgum bay.

All trees, both live and fire-killed, were tallied according to species for a 25-link width along these transects. Tables I and II

TABLE I.—Stem count and basal area per acre of live and fire-killed trees in Transect A

	Stem Count			Basal Area		
	Live	Dead	Total	Live	Dead	Total
Taxodium distichum	26	3	29	10.491	.096	10.587
Nyssa sylvatica	358	27	385	139.505	8.348	147.853
Cyrilla racemiflora	11	3	14	.693	.096	.789
Magnolia virginiana	125	6	131	23.253	2.456	25.709
Gordonia lasianthus	25	3	28	2.302	.035	2.337
Persea borbonia	9	0	9	.475	0	.475
Cephalanthus occidentalis	2	1	3	.074	.053	.127
Ilex cassine	222	20	242	6.516	.395	6.911
Acer rubrum	108	22	130	5.551	1.414	6.965
Desmothamnus lucidus	1	0	1	.018	0	.018
Grand Totals	887	85	972	188.839	12.910	201.749

show the stem count and the basal area per acre of the tallied trees by species.

As shown in these two tables the shrubby species, such as titi, hurrah bush and buttonbush sustained the greatest kill. The ratio of the live to the fire-killed trees in the basal area column shows that the larger trees were not killed to any great extent.

EFFECTS OF THE SEVERE BURNS

There is no known place in the swamp where the 1954-1955 fires burned severely enough over a large enough area to result in a prairie or lake. Coppice is rapidly restori · the forest that was killed in the more severely burned spots.

Usually severe burns were small and spotty but three such burns were fairly extensive: one in an area between Billy's Lake, Minnie's Island and Hickory Island; another north and west of Soldier Camp Island; and the third north of Suwannee Canal, between Camp Cornelia and Mizell Prairie. There were about 500 acres in each of these areas. Except for surviving roots, nearly all the trees in each were killed.

In order to have a record of the plant succession following the fire, sample one-acre plots were staked out in each of the severely burned areas (Fig. 1, C, D, E). Each plot was 10 chains long and one chain wide. All live and fire-killed trees as much as one inch in diameter at four and one-half feet above the ground were measured and recorded to indicate the composition of the forest prior to the kill. Probably some of the smaller trees were burned away and could not be measured.

Billy's Lake Burn.—The area north of Billy's Lake was covered by typical blackgum-bay forest. The peat depth in this plot averages about eight feet. The surface peat was burned away in spots as much as a foot or more.

TABLE II.—Stem count and basal area per acre of live and fire-killed trees in Transect B

	Stem Count			Basal Area		
	Live	Dead	Total	Live	Dead	Total
Taxodium distichum	8	2	10	5.432	.148	5.580
Nyssa sylvatica	234	70	304	95.846	7.525	103.371
Pinus elliottii	0	4	4	0	.160	.160
Cyrilla racemiflora	47	79	126	2.673	4.539	7.212
Magnolia virginiana	148	134	282	40.710	12.650	53.360
Gordonia lasianthus	28	31	59	3.252	4.877	8.129
Persea borbonia	50	54	104	7.530	8.022	15.552
Cephalanthus occidentalis	2	2	4	.074	.053	.127
Ilex cassine	12	2	14	.830	.196	1.026
Acer rubrum	18	38	56	3.170	4.187	7.357
Desmothamnus lucidus	3	50	53	.070	1.091	1.161
Grand Totals	550	466	1016	159.587	43.448	203.035

Fig. 4.—Recovery of woody growth three years after severe burning near Billy's Lake.

The composition of the resprouts is essentially the same as was the composition of the forest prior to the fire (Table III). The table does not reflect the true composition of the underbrush prior to the fire because much of this was burned away and could not be measured.

Suwannee Canal Burn.—Prior to 1932, the cover along the north side of the Suwannee Canal had been predominantly pond cypress and slash pine. Most of the timber was killed by fire during the 1932 drought. By 1954 the area had regrown in a dense thicket of pond cypress, bay, hurrah bush, titi and bamboo vine. The Mule Tail fire of November, 1954, followed by the fire of March, 1955,

TABLE III.—The number of stems, basal area, and sprouts of trees and shrubs in Billy's Lake plot

	Number of Stems		Basal Area		Sprouts
	Live	Fire-killed	Live	Fire-killed	
Taxodium distichum	0	8	0	.675	1
Gordonia lasianthus	0	430	0	65.524	56
Ilex cassine	0	37	0	2.773	13
Magnolia virginiana	0	137	0	13.922	36
Cyrilla racemiflora	0	125	0	5.846	39
Desmothamnus lucidus	5	5	0	.030	4
Nyssa sylvatica	0	135	0	39.421	38
Persea borbonia	0	7	0	1.085	14
Acer rubrum	0	10	0	.986	3
Clethra alnifolia	0	0	0	0	2
Itea virginica	0	0	0	0	23

burned away this brush and killed the few surviving large trees. The peat here was about six feet thick. About one foot of this burned away.

By 1958 woody growth was re-established sparsely (Table IV). The recovery here is less evident than in the burns at Billy's Lake or Soldier Camp Island, probably because this area had been severely burned in 1932 and then reburned in the recent fires. Possibly another such fire here would result in prairie.

Soldier Camp Island.—Prior to the fires, the forest on this area was predominantly pond cypress. The Mule Tail fire of November, 1954, killed or severely burned much of the timber and underbrush. By the time the fire of 1955 swept through, this dead underbrush had dried to the extent that it was much more flammable, and the intensity of the burning was such that nearly all surviving trees were killed.

The peat was shallower than average in this particular area; usually less than two feet in depth. This peat bed was entirely consumed. However, since the peat was shallow, the roots of most of the trees and shrubs reached the underlying sand and were partially protected. Root survival was such as to result in a substantial regrowth as shown in Table V.

PLANT SUCCESSION IN THE SEVERELY BURNED AREAS

All ground cover in both the Suwannee Canal plot and the Soldier Camp Island plot was mapped in 1956. The Suwannee Canal plot was remapped in 1957 and again in 1958. The Soldier Camp Island plot was remapped in 1958. Usually the cover was mapped and recorded according to species. In those cases where the cover was a mixture of two or more species, it was mapped as an association and the percentage of each species was estimated. The submerged

TABLE IV.—The number of stems, basal area and sprouts since the fires of trees and shrubs in Suwannee Canal plot

	Number of Stems		Basal Area		Sprouts
	Live	Fire-killed	Live	Fire-killed	
Taxodium distichum	1	29	1.396	3.993	14
Pinus elliottii	0	8	0	4.855	1
Magnolia virginiana	0	43	0	.880	18
Ilex glabra	0	4	0	.056	11
Gordonia lasianthus	0	19	0	1.416	0
Persea borbonia	0	29	0	.575	18
Ilex cassine	0	3	0	.093	0
Nyssa sylvatica	0	1	0	.006	5
Leucothoe racemosa	0	0	0	0	12
Itea virginica	0	0	0	0	76
Vaccinium arkansanum	0	0	0	0	2
Desmothamnus lucidus	0	0	0	0	35
Arsenoccus ligustrinus	0	0	0	0	1

TABLE V.—The number of stems, basal area and sprouts since the fires of trees and shrubs in Soldier Camp Island plot

	Number of Stems		Basal Area		Sprouts
	Live	Fire-killed	Live	Fire-killed	
Pinus elliottii	0	793	0	28.960	2
Taxodium distichum	4	650	2.650	59.854	53
Myrica cerifera	0	0	0	0	1
Magnolia virginiana	0	9	0	.711	12
Persea borbonia	0	27	0	.296	74
Ilex glabra	0	0	0	0	4
Ilex coriacea	0	0	0	0	1
Gordonia lasianthus	0	22	0	.389	2
Nyssa sylvatica	0	283	0	4.391	20
Clethra alnifolia	0	0	0	0	32
Desmothamnus lucidus	0	0	0	0	33
Arsenococcus ligustrinus	0	0	0	0	1
Itea virginica	0	0	0	0	1

aquatic plants, sphagnum and bladderwort, which occupied nearly all of the area not occupied by other plants, were not recorded. Tables VI and VII show the percentage of ground cover by species as mapped in these plots.

The year after the fire, herbaceous growth on the Soldier Camp Island plot was predominantly paintroot and beakrush. By 1958

Fig. 5.—Sparse recovery of woody growth in repeatedly burned area near Suwannee Canal. This would probably become prairie with one more severe burn.

this cover had been largely replaced by a variety of other herbaceous plants, a sedge, hardhead, fern and bur marigold being the predominating species.

By 1957, paintroot had invaded a considerable part of the Suwannee Canal plot. In 1958 this plant was replaced largely by

TABLE VI.—Soldier Camp Island plots showing per cent coverages in 1956 and 1958

Trees and Shrubs	*1956*	*1958*
Pinus elliottii	0	t
Taxodium distichum	.03	.37
Smilax laurifolia	.01	.08
Smilax walteri	0	t
Myrica cerifera	0	t
Magnolia virginiana	.01	.12
Persea borbonia	.05	.41
Ilex glabra	.01	.03
Ilex coriacea	0	t
Gordonia lasianthus	0	.01
Nyssa sylvatica	.01	.59
Clethra alnifolia	0	.16
Desmothamnus lucidus	0	.20
Vaccinium arkansanum	0	t
Itea virginica	0	t
Herbs		
Woodwardia virginiana	*	10.93
Sagittaria graminea		1.53
Andropogon sp.		t
Panicum sp.	.05	.33
Unidentified grasses		.11
Rhynchospora fascicularis	**	.77
Unidentified sedge	.09	8.69
Xyris sp.		5.92
Pontederia cordata	.06	.50
Gyrotheca tinctoria	50.79**	7.33
Hypericum spp.		1.54
Hypericum virginicum		.78
Ludwigia lanceolata		.79
Rhexia virginica		.77
Mint		.79
Bidens coronata		2.89
Eupatorium capillifolium		.78
Pluchea foetida		.77
Solidago fistulosa		t

* In 1956 there was a fringe of ferns at the base of most trees and stumps, the amount of which was not estimated.

** In 1956 this cover included a mixture of *Rhynchospora fascicularis* which had almost disappeared in 1958.

fern and sedge. Hardhead, which was a predominant species in 1956, had nearly disappeared by 1958. Just as in the Soldier Camp Island plot, sedge had steadily increased.

Of the species recorded in these plots, paintroot is of considerable value as a food for sandhill cranes and ducks. Apparently this plant was temporarily favored by the burn but it is rapidly being replaced by less desirable species. Bur marigold, a fair duck food plant, had increased on both areas by 1958.

As would be expected, coppice growth of the woody species has increased steadily since the fire.

EFFECTS ON ANIMAL LIFE

The effects of the drought and fires of 1954-55 on animal life of the Okefenokee Swamp have been varied. Some forms, notably fish and some animals directly dependent upon fish, were adversely affected. Other forms were not appreciably affected, or were actually favored.

Fish.—Okefenokee Swamp has long been famous for its sport fishing. The principal species taken are largemouth bass (*Micropterus salmoides*), bluegill sunfish, (*Lepomis macrochirus*), warmouth sunfish (*Chaenobryttus coronarius*), flyers (*Centrarchus macropterus*) and pickerels (*Esox niger*). Catfish (*Ictalurus nebulosus*) and mudfish (*Amia calva*) are also commonly taken.

TABLE VII.—Suwannee Canal plot showing per cent of ground cover by species in 1956, 1957 and 1958

Trees and Shrubs	1956	1957	1958
Pinus elliottii	0	0	t
Taxodium distichum	0	.24	.23
Magnolia virginiana	.05	.35	.90
Persea borbonia	.05	.30	.54
Nyssa sylvatica	0	.04	.05
Smilax laurifolia	.15	.17	.20
Itea virginica	.07	.44	.75
Desmothamnus lucidus	.34	.75	.63
Leucothoe racemosa	.01	.06	.24
Arsenococcus ligustrinus	0	0	t
Vaccinium arkansanum	0	.02	.01
Ilex glabra	.01	.08	.09
Herbs			
Woodwardia virginica	3.83	9.57	9.82
Carex sp.	16.25	46.07	52.46
Dulichium arundinaceum	.07	.43	t
Andropogon sp.	0	0	t
Gyrotheca tinctoria	0	9.57	.03
Peltandra virginica	.01	.01	.03
Xyris sp.	21.07	1.86	.51
Ludwigia lanceolata	1.28	18.25	0
Bidens coronata	0	0	.53

By November, 1954, the water level in the swamp was the lowest on record. The gauge reading at Camp Cornelia was 117.56 and at Billy's Lake it was 110.44. This was about four feet below normal, which means that most of the lakes and 'gator holes were dry or nearly dry. Naturally, fish concentrated at the few remaining places where there was water, as did also fish predators. The numbers of fish were sharply reduced. With the return of higher water levels, the decimated fish population was dispersed.

While the drought ended in the summer of 1955, the water levels remained comparatively low until June, 1957. Except for brief rises in March and May, 1956, the gauge readings at Camp Cornelia usually remained below 120.5 feet and the readings at Billy's Lake below 114 feet. When the water in Okefenokee remains at this low level, the acidity is high. pH readings were usually well below 4.5. Most fish do not reproduce readily in water as acid as this (Spector, 1956:457). It was not until April, 1957, that there was enough rain to raise the swamp water level to normal and to modify acidity enough to permit fish reproduction.

There was virtually no fishing in 1955. Since then, sport fishing has improved steadily. Catches in 1958 were reported to be the best in more than ten years.

Frogs.—If the frog population was reduced by the drought, it was not evident the following year. The cricket frog (*Acris gryllus*) is the most abundant vertebrate animal in the Okefenokee Swamp. These frogs are distributed throughout the area. Doubtless they are an important item of food for the Okefenokee wading birds.

The pig frog (*Rana grylio*), bronze frog (*Rana clamitans*), leopard frog (*Rana pipiens*) and the green tree frog (*Hyla cinerea*) are also numerous in the swamp. The squirrel tree frog (*Hyla squirella*), the grass frog (*Hyla ocularis*) and the pine woods tree frog (*Hyla femoralis*) are common on the swamp edge and on the islands.

Snakes.—While the abundance of cotton-mouth moccasins (*Agkistrodon piscivorus*) in the Okefenokee Swamp has been grossly exaggerated in popular literature, it is true that this species is the swamp's most common snake. Apparently the drought affected cotton-mouths adversely, as they were rarely seen the year afterward. When the swamp dried out, these snakes concentrated at the few places where there was open water, where they fell victims to predators. By 1958, cotton-mouths were seen oftener than in any year since the drought and it seems likely that their numbers are approaching those of the pre-drought population.

Alligators.—It does not appear that the alligator (*Alligator mississippiensis*) population was reduced by the drought and the fires. Probably they actually thrived on conditions brought about by the drought. These reptiles concentrated at the few remaining open water areas as did their prey — fish, turtles, otters, raccoons and birds.

There are no pre-drought figures on alligator populations but residents of the swamp area do not believe that the number of alligators was reduced by the drought. On a trip along the fifteen-mile water course between Camp Stephen Foster and upper Big Water, on a warm day in time of low water, a careful observer can often count as many as 4 alligators per mile. As many as 91 were counted along this course in a one-way trip October 23, 1958. They may be seen at about the same frequency along the Suwannee Canal. Forty-eight were observed along seven miles of this canal, November 20, 1958.

Otters.—There is no practical way of censusing these animals (*Lutra canadensis*) in the Okefenokee. However, we do know that the swamp's otter population was drastically reduced during the drought. Before the drought these mammals were commonly reported. Since the drought, they have been rare. During the years 1957 and 1958, only 14 of them were reported by refuge personnel, who spent not less than 100 man-days on patrols along refuge water courses on the alert for wildlife.

It is believed that the alligator was a major cause of the reduction in the number of otters. During the drought, otters concentrated at the few places in the swamp where there were water and concentrations of fish, with the result that they became easy victims of the alligators.

Raccoons.—Prior to the drought, the raccoon (*Procyon lotor*) was the most abundant large mammal in the Okefenokee Swamp. Like the otter, and probably for the same reasons, its numbers were drastically reduced during the drought. By the fall of 1958, the raccoon population had recovered and this animal is again abundant.

Bears.—The Florida black bear (*Euarctos floridanus*) was not numerous before the drought nor has it been since. According to refuge personnel and other residents in the vicinity of the swamp, there is no noticeable difference in their numbers just prior to or since the drought. There were 14 bears reported killed on the west side of the swamp in 1957 and 11 reported killed in the same area the following year. This is comparable to the estimates of kills before the drought. Fleetwood (1947) reported the following kills on the west side of the swamp from 1941 to 1946: 1941, 6; 1942, 10; 1943, 9; 1944, 4; 1945, 1; 1946, 19. Francis Harper (1927) estimated that an average of about twelve bears were killed annually.

Sandhill cranes.—There is no evidence that the sandhill crane (*Grus canadensis*) population in the Okefenokee was reduced by the drought or the fire. On the contrary, conditions since the drought appear to have been favorable to this bird. Crane counts made before and after the drought indicate that the resident population is about the same as it was before the drought and that the winter population is much greater.

In 1921, Francis Harper estimated that the sandhill crane population of Okefenokee was about 100 (Walkinshaw, 1949). Thomas and James Roddenberry counted 94 cranes in Chase Prairie from January 24 to 27, 1935 (Hebard, 1941). During a day spent in Chesser and Chase prairies in 1945, Dr. Walkinshaw and Ben Chesser counted 26 cranes. Raymond J. Fleetwood estimated that the swamp crane population was about 300 during the winter of 1947 and 1948. In ten trips into Chesser and Grand prairies that winter, his counts varied from 20 to 71.

These counts appear low when compared with recent counts.

On January 29, 1957, Dock A. Rider and I counted 522 in Chesser Prairie alone. During the winter of 1956-1957 in any day spent in Chesser and Grand prairies, an observer could see 100 or more cranes. It was estimated that the swamp's population was about 1000. The increase of paintroot, a favorite crane food, may have attracted this unusually large concentration of winter visitors. It is also likely that the normal winter population was augmented by migrants which ordinarily would have wintered in the Florida prairies which were dry at that time.

Water levels during the winter of 1957-58 were about normal. The crane population of that winter, while considerably below that of the previous winter, appears to have been higher than that of the winters prior to the drought. In five trips made during that winter from November to February across Chesser and Grand prairies, counts varied from 39 to 79 cranes. On December 20, 1958, Raymond Johnson and I counted 191 during a whole day spent in Chesser Prairie.

Herons.—The common egret (*Casmerodius albus*) is the most abundant heron in the Okefenokee Swamp. Its numbers in different parts of the swamp vary with the seasons and with changing water levels so that comparisons of estimates before and after the drought do not make a very reliable basis for evaluating the effects of the drought and the fires on this species. Apparently its population has been affected little.

Fleetwood reported from 32 to 206 in trips across Chesser Prairie in 1947 and 1948. Carter reported an average of 25.0 observed in May, 1942 and 12.7 in June and July, 1942. These compare with observations made since the drought when six counts made in Chesser and Grand prairies through May, June and July in 1957 and 1958 averaged 25.5 individuals per trip. Ten trips made from September to December, 1957 and 1958 averaged 79.2 individuals per trip.

Two common egret rookeries, one near Chesser Island and one near the northern part of the swamp, which were thriving prior to the drought, have been non-existent since. However, there may be active rookeries in remote parts of the swamp which have never been found. One rookery at Steedley Bay, three miles northeast of

Fargo, which has been active for many years, had about 200 nests in 1958. There is no reliable estimate of the size of the rookery in past years.

There is no evidence that the population of great blue herons (*Ardea herodias*) has been changed as a result of the drought or fire. Out of 37 trips made into Chesser and Grand prairies during 1957 and 1958, an average of 1.8 herons per mile was observed. A few are always seen but they are never very numerous. Observations ranged from 0.1 to 6.1 herons per mile.

This compares with Carter's (1940) estimate of from 2 to 20 observed on a usual trip in the prairies. His trips probably covered from six to ten miles. Fleetwood reported that eight individuals were the most observed by him on any one trip into the swamp in the fall of 1947.

The green heron (*Butorides virescens*) population at Okefenokee apparently varies annually. Carter's reports of 1940 indicate that they were not particularly numerous that year but in the spring of 1942 there were 29 nests along Suwannee Canal at Camp Cornelia. During the years 1956, 1957 and 1958 these birds were fairly common, but not numerous, along Suwannee Canal. Judging from reports, the heron is certainly much less numerous than it was in 1942, but there is not sufficient evidence to indicate whether these numbers were affected by the drought or fires.

Ibises.—Wood ibises (*Mycteria americana*) are regular summer and fall visitors at Okefenokee. There is no evidence that the fires have resulted in more or less favorable conditions for them. Apparently the population varies with the water levels of the swamp. When water levels are low so that the prairies are only partially flooded, wood ibises become numerous in the fall, probably because they are attracted to the swamp by more readily available food. In the fall of 1956, the water levels were low and wood ibises were common. The following year water levels in the swamp were near normal and only a few were observed. In the fall of 1958, water levels were again low and wood ibises were again quite common.

The white ibis (*Eudocimus albus*) is an uncommon summer resident and, in years of low water, an abundant fall and early winter resident. During the fall of 1958, usually from 50 to 100 white ibises would be seen on a trip across Chesser and Grand prairies or on a trip to Big Water. On December 20, 1958, 522 ibises were reported in Chesser, Mizell and Chase prairies. This compares with Fleetwood's reports of several flocks ranging from 25 to 175 individuals during the spring of 1947. In 1948, from January through April, a time of unusually high water levels, Fleetwood reported four observations, ranging from four to fifty white ibises.

Waterfowl.—The prairies are the favorite feeding ground in the swamp for ducks. The 1954-55 fires, which burned over these areas only lightly, had no enduring effect.

Favorite waterfowl plants such as paintroot and smartweed intruded into the more severely burned places in the bays and houses but the area of such burns was so small that there has been no appreciable difference in waterfowl use.

The wood duck (*Aix sponsa*) is the only duck which is a permanent resident of the Okefenokee. During the spring and summer some four or five pairs are usually seen in a day spent in the swamp. In the fall and winter, over a hundred may commonly be seen during a day spent in the prairies. This is comparable to counts made by Fleetwood in 1947 and 1948 and by Carter in 1942.

The most numerous duck at Okefenokee during the fall and winter is the mallard (*Anas platyrhynchos*). An unusual observation was made by Jewett Hall and W. C. Cone who estimated about 2400 in Floyd's Prairie, on January 14, 1958. Ordinarily, several hundred will be seen in a day spent in Chesser, Grand, Mizell, Chase or Floyd's Prairie. They are usually to be seen in flocks of less than a hundred but they are sometimes more numerous. This compares with Fleetwood's reports of small flocks ranging up to 186 individuals through January and February, 1948. He reported a total of 571 seen January 9, 1948 in Chesser, Grand, Hog Island, Buck Lake, Chase, Floyd's and Sapling prairies by four parties. Carter reported that counts ranged from 100 to 500 in January and February, 1941.

Other ducks commonly observed in small numbers are the black duck, pintail, American widgeon, green-winged teal, shoveler, blue-winged teal, ringneck, lesser scaup, and bufflehead. These are the same species commonly seen before the 1954-55 drought and fires.

REFERENCES

CARTER, H. A. 1940, 1942. Okefenokee National Wildlife Refuge Biological Reports. Unpublished.

FLEETWOOD, RAYMOND J. 1946, 1947. Okefenokee National Wildlife Refuge Biological Reports. Unpublished.

HARPER, FRANCIS, 1927. The mammals of the Okefenokee Swamp region of Georgia. *Proc. Boston Soc. Nat. Hist.*, **38**(7):191-396.

HEBARD, FREDERICK V. 1941. Winter Birds of Okefenokee and Coleraine. *Georgia Soc. Nat. Bull.*, **3**:84 p.

HOPKINS, JOHN M. 1947. Forty-five years with Okefenokee Swamp. *Georgia Soc. Nat. Bull.*, **4**:69 p.

MACNEIL, F. STEARNS, 1949. Pleistocene shore lines in Florida and Georgia. *Geol. Survey Professional Paper*, 221-F:95-106.

MOORE, ROY. 1955. Field Report of Fire. Okefenokee National Wildlife Refuge Fire No. 1955-1. Unpublished.

SPECTOR, WILLIAM S., editor. 1956. Handbook of biological data. W. B. Saunders Co., Philadelphia. 485 p.

WALKER, LAURA S. AND SARA S. KING. 1947. Old Okefenok. Foote and Davies, Inc., Atlanta, Georgia. 73 p.

WALKINSHAW, LAWRENCE H. 1949. The sandhill cranes. *Cranbrook Inst. Sci. Bull.*, **29**:202 p.

Notes and Discussion

An Interesting Growth Relationship Between Two Specimens of Erythrina sandwicensis

A remarkable growth relation between two wiliwili trees (*Erythrina sandwicensis* Degener) was observed on Haleakala Mountain, Island of Maui, Hawaii. The trees which are endemic to the Hawaiian Islands occur in this area in two color phases, bright orange and pale yellow. While collecting seed from one of these groups of trees I observed what appeared at first glance to be a yellow-flowered branch rising from an otherwise red-flowering tree. Examination showed that a lower limb of the yellow flowering tree had at some time previous, grown between two branches of the red-flower tree so that the limb rested in its crotch. Subsequent growth in diameter of the two trees had caused the limb of the yellow-flowered tree to become totally encased in the crotch of the red-flowered tree.

In spite of the total encasement, both trees were still growing and apparently quite healthy. Specimens were not taken as it would be of interest to see what would be the ultimate fate of these trees.

In view of the large amount of tissue of the red-flowered tree, and the vigor of the yellow-flowered branch passing through it, it is of interest to ask whether a natural graft was formed between the two trees. The situation is remarkable since, by chance, two trees of one species, each with different colored flowers were involved.—E. J. Britten, Associate Agronomist, Hawaii Agricultural Experiment Station.

Book Reviews

MAMMALS OF WISCONSIN. By Hartley H. T. Jackson. The University of Wisconsin Press, Madison. 1961. xxii + 504 p. $12.00.

Many hours of field and laboratory investigations have culminated in this study of Wisconsin's mammalian fauna. Although organized in the form of a typical state list, this book goes beyond the "ordinary" in the scope of its coverage. The detailed treatment of the individual species with respect to: identification, habits, habitat and status is a welcome review of the literature of the Wisconsin taxa through 1959. Cogent observations, accumulated through the author's long field experience, are interestingly incorporated throughout. The book is profusely illustrated with excellent photographs and diagrams depicting pertinent identification characters and natural history observations from various sources.

It is difficult to find much in this book with which one might take issue. However, a few points might be mentioned. There is an inconsistency of usage with regard to the abbreviation of the word "premolar" in the dental formulae; in the introduction PM is used, whereas in most of the text the standard P, is used. Despite the wealth of illustrations mentioned before, there might have been more palatal views of teeth, to acquaint the novice with many of the standard characteristics used in identification.

Of particular interest to this reviewer is Dr. Jackson's division of the state into three "life zones" based on mammalian distributions: Canadian in the northern one-third; the Upper Austral extending from the southeastern corner by a narrow spit across the state and up the western side paralleling the Mississippi River; and the remainder, the Transition. In the Introduction these zones are typified by certain plant and animal species; in some cases, plant forms of questionable value as "characteristic" organisms have been used. For example, balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*) are used as characteristic of all of the Canadian zone when in actuality these are characteristic dominants of only a small section of Boreal forests in the extreme northwestern part of the state; also the use of hackberry, *Celtis occidentalis*, and pecan, *Carya illinoensis*, as characteristics for his Upper Austral zone is tenuous when both are rather uncommon in this region, the latter at best just reaching the state.

This is not the place for a full discussion of biogeography, but it might have been ecologically more meaningful to consider the relations of the mammalian distributions to those of the plants as presented by J. T. Curtis in his recent book, *The Vegetation of Wisconsin*. A cursory glance at the mammal distribution maps indicates the possibility of a "tension zone," quite comparable to that presented for plants by Curtis. Also, interpretations of the mammal distributions based on only the three broad zones, obscures any consideration of factors such as the prairie influence in the southwestern corner of the state.

These are only minor points, and in no way detract from the value of this handsome book. It is a comprehensive and lucid presentation of the mammalian fauna of this most interesting transition state. Dr. Jackson has not merely collated the available knowledge of these mammals, but has digested this information and presented it in a usable form. This book will be ranked among the outstanding state lists and hailed as a compendium of mammalian natural history.

Mammals of Wisconsin is recommended, without reservation, for any student of Wisconsin natural history and for all people, whether amateur or professional, who are interested in mammals.—JAMES A. MACMAHON, Department of Biology, University of Notre Dame, Notre Dame, Indiana.

THE PLANT COMMUNITY. By Herbert C. Hanson and Ethan D. Churchill. Reinhold Publishing Corporation, New York. 1961. 218 p. Illus. $4.95.

The authors state in the preface that they, "have adopted as the central theme of this book the formation and nature of the plant community." This is a formidable undertaking as the nature of the community is certainly one of the most complex of ecological problems. The concept of communal relations among organisms and their relations to the environment is fundamental to ecology and an adequate understanding of community concepts is essential to any view of ecology. The authors' predilections as to the nature of the plant community and the means by which it may be described, analyzed and synthesized into a comprehensive and comprehensible intellectual structure are of particular importance in view of their choice of theme.

The book is divided into four parts: 1. Species and populations, two chapters on ecological characteristics of species and the grouping of species; 2. The community, two chapters on analytic and synthetic characteristics used in describing the community; 3. The dynamics of communities, one chapter; 4. Classification of communities, one chapter.

The first part of the book offers an excellent discussion of the ecological amplitude of species and emphasizes the genetic basis of species behavior. It is replete with examples from the literature and the authors' own work. It is noticeable here that the coverage is heavily weighted towards grassland. This continues throughout, as suggested by the following rough count of generic citations in the index: Abies 2, Acer 3, Agropyron 41, Andropogon 21, Betula 4, Bouteloua 36, Bromus 21, Picea, 4, Pinus 21, Poa 15, Quercus 15, Stipa 25. The requirements and competitive ability of species and the role of these in community organization are clearly and effectively handled.

The second part considers quantitative and qualitative methods of analysis and synthesis of communities. In general these are well stated and illustrated with appropriate examples although several usages seem inappropriate. Indices of similarity, such as that of Sorenson, should not be equated with measures of interspecific association. Such an index is more appropriately regarded as a synthetic characteristic since it commonly is used to compare two samples of vegetation or to construct a matrix among several samples. Even if used to compare samples within a single stand it does not serve as a measure of interspecific association as is suggested.

The introduction of the concept of density-dependent and density-independent factors as used by the animal ecologist seems to offer little advantage to the study of plant communities. The validity of the concept is in dispute among animal ecologists and its meaning is not clear. For example, in the present volume a density-independent factor is defined as ". . . one that has little or no effect on density (for example the CO_2 content of the atmosphere), because it rarely if ever influences the number of plants in an area." Another recent ecology textbook, Odum's "Fundamentals of Ecology" states (p. 209), density-independent aspects of the environment tend to bring about variations, sometimes drastic, in population density. . . ." Obviously the term is used in different ways which indicates the need for clarification and agreement among ecologists as to its meaning and validity. This confusion reflects the disparity of views existing among animal ecologists and plant ecology has no need of additional confusing terms.

The use of Raunkiaer's "normal" curve of frequency as an indication of uniformity or homogeneity has been the subject of much discussion in the past and, in the light of numerous criticisms of such use, it is surprising to find it suggested here as a test of uniformity within a stand and of homogeneity in

a community type. The very brief discussion of the species-area curve does not serve to make the concept clear to a novice ecologist nor does the simplified coverage allow the necessary qualifications. No citations to the relevant literature are given.

It is unfortunate that some of the problems of ecological terminology persist although this certainly cannot be laid to the authors of the present volume. Abundance, is used by them as synonymous with population density (number of individuals) while Cain and Castro in the recent "Manual of Vegetation Analysis" restrict its meaning to estimated numbers or the less frequently used average number of individuals per quadrat of occurrence.

Part three considers community dynamics including relation of communities to environmental gradients and habitat patterns, successional changes and non-directional changes in community composition. The authors adopt a view of climax as consisting of a pattern or mosaic of vegetation distributed on an environmental gradient.

The authors' views on the nature and classification of communities which are explicitly covered in part 4, but appear implicitly throughout, lean heavily upon the precepts of various European phytosociologists. A statement in the conclusion summarizes these views concisely. "Classification, however, when analytic data on intrinsic properties and descriptions are available, may begin with the basic units, which are usually small in area and homogeneous." The assumption that vegetation consists of small or large, homogeneous, basic units which can be identified and classified is one of the classical views of plant ecology and has many distinguished adherents. The authors are eminently justified in adopting and propounding these concepts. However, they do their prospective audience an injustice in that alternative views are given short shrift, and data supporting them is unrepresented or under represented. Gleason's "Individualistic Hypothesis" is dismissed, on page 67, as impossible but no adequate consideration is given here, or at any other point, to a decade of work in Wisconsin summarized by Curtis as ". . . conclusive proof of Gleason's individualistic hypothesis of community organization. . . ." Nor is the work of Whittaker, or Goodall which buttresses Gleason's hypothesis, cited in this context although, it is referred to in other circumstances. The not inconsiderable European literature paralleling Gleason's views is ignored.

The extensive work of the past ten years relating to ecological gradients is similarly dismissed, "The ecological gradients of importance to vegetation are unknown at the beginning of an investigation of the vegetation of an area and cannot be guessed before hand, so the ordination of communities according to ecological gradients is very difficult. There appears to be general agreement that the basis for securing understanding of nature must be the study of directly observable characters, and not hypothetical inferences about the relations between vegetation and environment." The establishment of meaningful gradients or orders is by no means so difficult, as evidenced in the work of Curtis, Bray, Goodall or Whittaker, none of which is cited in this context.

However, on page 172, the existence of gradients is attested, species composition gradually changing in response to decrease in soil moisture. The cline is segregated into units quantitatively on the basis of arbitrarily chosen values of cover and frequency for selected pairs of species. It is at least as likely that a meaningful ordination could be constructed and the cline then subdivided secondarily. The establishment of units initially, simply obscures the cline or gradient and valuable information concerning species behavior and changes in community composition may be lost.

In short, the case for a well defined series of community types is presented

without adequate attention to controversial viewpoints. Controversial viewpoints, as Egler noted a number of years ago, being "what the other fellow thinks: fundamental real basic facts are what the writer knows are true." It is interesting to note that the traditional problem of how similar "similar" (p. 71, 174) communities must be in order to be recognized as members of a community type is not adequately elucidated at any point. The example cited in chart 2 (p. 19) seems to represent a completely subjective segregation of community types and from the data offered could be readily divided into several other sets of communities or interpreted as a continuum. Certainly in itself it lends no conviction to the authors' thesis.

It is perfectly true, as the authors suggest that accepting the view of vegetation as varying continuously does not preclude the possibility of recognizing community types on the basis of arbitrary criteria if this is desirable. However, it should be clear what these criteria are. To attest to the utility of such classification by an analogy of the segregation between youth and old age can only leave those of us who range in the middle aged class to wonder how recently we left youth or how soon we arrive at old age, or whether to use chronology or "you're as old as you feel" as a yardstick.

The text is in general clear and few errors were noted, although occasional statements give some difficulty, viz.: "The independence of a species may be greatly modified when it is growing in association with other species as compared to growing alone." (p. 59.)

"In some cases it is a continuum, in others a series of communities, or it may be a continuum in one period, a distinct community in another. In most cases elements of both are present in varying proportions." (p. 69.)

"The environment is a controlling influence, not a property of vegetation and the successional status is often hypothetical, though important." (p. 173.)

The book is illustrated with well selected photographs largely from the files of the U.S.D.A. Numerous references to the British and Scandinavian ecological literature are given.

The Plant Community is designed for a one semester course in plant ecology, a supplement to textbooks in general ecology, as an adjunct to courses in various related subjects or for the general reader. Its use as a supplement to other texts, or selected readings is quite feasible. As a single volume text its utility is limited by the brevity of its coverage of difficult aspects of community analysis and synthesis and by an inadequate evaluation of current views of the nature of the community.—ROBERT P. MCINTOSH, University of Notre Dame, Notre Dame, Indiana.

THE USE OF CHEMICALS IN SOUTHERN FORESTS. Edited by Robert W. McDermid. Louisiana State University Press, Baton Rouge. 1961. v + 152 p. Illus. $4.00.

This volume contains the published proceedings of the Ninth Annual Forestry Symposium held at Louisiana State University. It is composed of three parts: "Forest Fertilization." "Using Chemical Herbicides in Southern Forests" and "Chemical Use in Forest Protection."

Forest fertilization is fresh pasture in American forestry and its denizens are characteristically enthused about its provident potentialities. This is both admirable and dangerous. It is demonstrable that trees respond to artificially applied mineral amendments and that the nature of such response, in certain cases and under conditions of severe nutrient deficiency, is often striking. Such phenomena warrant investigation. The deficiencies in our knowledge concern-

ing the duration of such response, the effect of mineral amendments on wood quality and quantity, competitive growth and pathogenic susceptibility are equally impressive and deserve to be remembered. At an even more fundamental level, an economic justification for undertaking forest fertilization on an extensive scale requires definition as does the "optimal" limits below which such measures should be resorted to.

On the whole, there is, among the authors of the present work, a gratifying cognizance of these fundamental deficiencies in our knowledge of the need for and effects of forest fertilization. The exercise of such disciplined awareness must, of necessity, continue to be an important part of the mental equipment of all those engaged in the field for some time to come, for the long-term nature of much of the research initiated on such problems (and here reported on in detail for southern pine forests) makes it unlikely that definitive results and recommendations will be forthcoming for a number of years.

As a source of information on the mineral nutrition of trees, the present work, while valuable, cannot compare with the published proceedings of a similar symposium held at Duke University in 1958 (School of Forestry Bulletin No. 15, 1959).

It is curious that the knowledge accumulated in the last 25 years on the mineral nutrition of citrus crops, pecan, tung and other horticultural species receives no mention in the present volume.

Methods employed in the basal and foliar application of herbicides for the control of undesirable woody growth are given informative treatment in Part II. The use of aircraft in the extensive application of herbicides in the South is thoroughly covered. A short but pithy account of Mr. J. A. Kirch on the absorption, translocation and ultimate toxicity of the commoner herbicides in woody plants is as good an account of these matters as has appeared anywhere. It is followed by discussion of the necessary legal precautions that must attend the use of these chemicals.

The chemical warfare being waged on the "vicious triumvirate" — fire, insects and disease — is given an airing in Part III. Those whose interests revolve around the protection of forests will derive much encouragement from the accounts given of the relative efficiency of many of the implements in this chemical arsenal. But it is to be hoped that all of them will read the concluding and sobering article by Mr. J. L. George on the effects of widespread use of such chemicals on wildlife populations. A balanced accounting of the effects of such use has not yet been made. In terms of the greatest good and the wisest use of the resource, it may transpire that, in certain cases, the forester and his chemicals will have to stay at home.

Uniting as it does so many facets of man's involvement with the forest, this little volume is well worth the moderate sum required for its purchase. Its appeal is wider than the title would suggest. It will doubtless serve as an informative source for research workers actively involved with the use of chemicals in forest practice. — WILLIAM F. MURISON, Harvard Forest, Petersham, Massachusetts.

THE DOUBLEDAY PICTORIAL LIBRARY OF NATURE. Edited by James Fisher, Sir Julian Huxley, Sir Gerald Barry and J. Bronowski. Doubleday and Company, Garden City, New York. 1960. 359 p., illustrated. $9.95.

All too often "nature books" attempt to amaze, astound or thrill their readers; all too few attempt to be truly informative. Even those which are factually reasonably accurate are often written with a liberal supply of exclama-

tion points and superlatives, or with the implied attribution of human emotions and motives to organisms that obviously cannot possess them. (I find it difficult for example, to believe that a pitcher plant can be guilty of treachery.) And even a well written nature book usually leaves the reader only a set of perhaps very interesting, but nevertheless mostly unrelated, facts about a miscellany of odds and ends. Except for actual textbooks and others with a similar pedantic approach, very few efforts are made to provide information about the basic phenomena that underlie all aspects of nature; an even smaller number have succeeded in doing so in a thoroughly interesting and readable manner. This volume is one of the select few.

As stated on the dust jacket, this book is "the story of our planet Earth and the life upon it." Obviously no book of 359 pages, even when provided with multitudinous pictures presumably worth ten thousand words each, can do full and complete justice to a subject of such scope. The editors have, however, exercised excellent judgment in their choice of material for inclusion, and have put together a well balanced volume. Generalizations and simplifications are never carried to the point of actually misleading the reader, as can so easily happen. The discussion of many subjects is not only accurate, but includes some of the more recent research and concepts developed by professional biologists and geologists that has not as yet found its way into many textbooks.

The style and manner of presentation are interesting and entertaining as well as informative. The many illustrations, ranging from simple line sketches to full color reproductions, are intimately woven together with the textual material. As might be expected from the list of editors and advisors, there is an indefinable, but unmistakable, British flavor, despite the careful Americanization of spellings and word usages. This, perhaps, is one of its advantages. The Europeans have, on the whole, been far more successful than Americans in popularizing scientific and scholarly subjects, making them intelligible and interesting to the lay reader without juvenilizing them. Only within the last few years have an appreciable number of American books of comparable intent and quality appeared.

In addition to the body of the text there is an appendix, though not titled as such, which includes about 25 pages devoted to a complete classification, to the ordinal level in some groups, to the class level in others, of the plant and animal kingdoms, and a glossary of about fourteen pages. Perhaps some idea of the scope and level of the book can be obtained from the fact that the "A's" in the glossary include such words as achene, adaptive radiation, allele, anaerobic, anastomosis, antibiotic, antigen, anticline, atoll and auxin.

This is the second in a series of eight projected volumes, the first having been the Doubleday Pictorial Library of Science.—J. A. THIEN, University of Notre Dame, Notre Dame, Indiana.

MARK CATESBY, THE COLONIAL AUDUBON. By George Frick and Raymond Phineas Stearns. University of Illinois Press, Urbana. 1961. x + 137 p. Illus. $5.00.

The British zoologist George Edwards wrote to Thomas Pennant that Catesby was "too modest to rise in the world by pushing his interest amongst the great, to many of whom he had access." This was twelve years after Catesby's death. His great folio work on the *Natural History of Carolina, Florida and the Bahama Islands*[1] was his consuming task and remains his monument.

[1] *Cf.* W. T. Stearn (*Jour. Soc. Bibliog. Nat. Hist.* **3**:328. 1958) for dates of issue not mentioned by authors.

Elliott Coues' verdict of 1878: "classic, conspicuous in merit *inter congeneres sui temporis*, and indispensable for occasional consultation" stands today.

For his pioneer account of birds, illustrated with one hundred plates, Catesby has been designated the founder of American ornithology. As Swainson remarked, he was the first author to launch natural history books in folio on the expensive subscription plan for which Audubon and Gould are justly famous.

Pulteney published the first biographical sketch of Catesby in 1791 and it was extensively quoted until Dr. Elsa Allen published fresh materials in 1951. Since then Phineas Stearns has written in fine detail of Petiver, and recently George Frick (*Bibliog. Soc. Amer. Papers* **54**:163-175. 1960) on some of the more disputed points in Catesby's life. These two professional historians, Frick of the University of Delaware and Stearns of the University of Illinois, have searched far and researched well to produce this handsome volume on Catesby the man and the naturalist, well documented, temptingly illustrated and, happily, modestly priced.

Someday Catesby's *Natural History* will be reissued, somewhat along the lines of William Vogt's edition of Audubon's *Birds of America*, if not more ambitiously. Perhaps to guide the editor of that hoped-for *redivivum* it may be germane to elaborate on some points raised in my brief review in *Science* (134:467. 1961). The most unsatisfied need in a study of Catesby now, as Elsa Allen remarked ten years ago, is to localize his movements in Virginia and Carolina toward as precise an itinerary as possible. This may have to wait for unfound manuscripts, and may indeed prove hopeless, but the plant collections he made survive, and if they were studied critically by a field botanist conversant with the habitats of the Carolina flora and an eye for those with restricted ranges, it might prove a long start in that search. The lack of any ticketed bird skins is unfortunate, but, judging from Audubon and to a lesser extent, Wilson, bird artists were not necessarily skilled birdskin preparators. Those original Catesby drawings preserved in the Royal Library at Windsor may carry some memoranda as to the time and place, or source of the materials illustrated.

Considering their period, Catesby's are good figures. There are several lapses (e.g. the heath hen with long ear tufts). Richardson, the art historian of Detroit, recently described the Catesby plates as "crudely engraved but nonetheless strong, decorative, and beautiful." The contemporary British art historian, Wilfred Blunt, is severe and accurate when he labels Catesby a "conscientious amateur." Ten of Catesby's bird plates are reproduced in black and white by Frick and Stearns.

The conchologist Guy Wilkins (1953) reported on Sir Hans Sloane's shell collection which by 1728 had reached a total of 4,911 specimens, the increase of the three previous years perhaps due to the return of Mark Catesby in 1726 from the New World. Catesby published only two terrestrial and two marine shells identified with the aid of Martin Lister's *Historia conchyliorum* which contained John Banister's Virginia contributions. Though Catesby's influence on insect taxonomy in the Linnaean period was negligible, he figured twenty-six insects, nearly half lepidopterous. In paleontology Catesby was preceded by John Banister who left descriptions of the backbone of a whale and of a number of fossil teeth, bones and shells. This was thirty-five years before Catesby described the grinders of an elephant.

There is some interest in Catesby's proposing Lieut. General James Oglethorpe as a member of the Royal Society. The authors remark on the Gen-

eral's plant collections from Georgia. In this connection it is interesting to recall that Dr. William Houstoun (d. 1733) would, had he lived, have botanized in Georgia at the instigation of Oglethorpe.

Catesby's botanical contributions were not slight. The authors treat them extensively in Chapter Six. John Martyn's sumptious folio work, the *History of Rare Plants*, reported on Catesby's novelties in 1728, only four years after his introductions had been planted at Chelsea. Martyn's *History*, by the way, consisting of fifty color plates, described by Pritzel as "elegantissimae certe sunt," has been compared with Catesby's own *Natural History* for its grand plan. The role of Catesby's illustrations in giving graphic validity to Linnaeus's new species published in the *Species plantarum* has been given its due recognition. Linnaeus gave scant attention to the dried plants brought back by Catesby for he was chiefly engrossed with the living plants growing in the Physick Garden at Oxford.

At times Catesby was an accurate observer: he wrote that Dahoon Holly (*Ilex cassine*) was "rare, seen only on Col. Bull's Plantation on Ashley River, where it grows in a bog." The Charleston naturalist, Laura M. Bragg, confirmed its rarity. Other Catesby descriptions she found "inadequate and unscientific." Leaf venation was often conventionalized beyond use in identification. James Edward Smith remarked that the want of a sketch of flower parts was the principal defect, but that the state of botany then did not suggest this to Catesby.

Peter Collinson was apprehensive of the cost of the Catesby folios as they appeared, and so perhaps it was he who encouraged Catesby to prepare a modest summary of his observations of 85 trees. This appeared first as *Hortus Britanno-Americanus*. Though Frick and Stearns insist that this work "was finished by Catesby shortly before his death," it shows the heavy hand of the publisher. It is interesting that the *Hortus*, published in 1763, sold lamely — Joseph Banks who zealously acquired such works missed it — and that it was repackaged four years later by a second publisher, but it continued to be ignored by the general public. It was indeed the *Natural History*, with its "broad appeal," that established Catesby's position. Catesby remained the standard authority through the eighteenth century. It is significant that Peter Collinson checked Bartram's discoveries bird by bird and plant by plant with Catesby. On the William Bartram drawings acquired by Lord Derby and preserved at Knowsley Hall may often be noticed the touchstone "Not in Catesby." Winterbotham wrote a four-volume *Historical . . . view of the United States of America* in his cell in debtor's prison and he refers to Catesby in noticing the "Hooping Crane," the "Flammant or Flamingo," the "Water-frog" (*Rana catesbeiana*), and the "Land-frog." Southey is said to have passed the books through the prison windows on a kind of interlibrary loan. At this point we may wince at the weight of a set of Catesby, if not at its rarity!

Frick and Stearns reaffirm Catesby's death evidently on conclusive grounds as 1749 rather than 1750. They uncovered a letter written by George Edwards to Thomas Pennant in 1761 in which Edwards remarks upon attending Catesby's funeral. There, the argument rests. Two centuries later we have an intriguing portrait of the man and his work.—JOSEPH EWAN, Tulane University, New Orleans.

INSTRUCTIONS FOR AUTHORS

In general the author should follow the recommendations of the *Style Manual for Biological Journals* distributed by AIBS at a nominal cost.

Manuscripts should be typewritten, doubled-spaced with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The initial page should contain the title, author's name, full mailing address and an informative abstract, not to exceed three per cent of the length of the manuscript. The abstract is published in lieu of a summary. Acknowledgments should be included in the Introduction. Do not underline any words except scientific and generic names.

References in the text should be cited by author and date, e.g., Smith (1960). In the Reference section, they should be listed alphabetically by authors' names. References to periodical literature should contain title, inclusive page numbers and the name of the journal spelled out. Book citations should include author's name, complete title, edition, name and location of publisher, the total number of pages.

A subsidy will be required for papers which exceed twenty journal pages in length and for tabular material in excess of two printed pages. Engraving cost in excess of ten dollars is charged to the author.

RECENT PUBLICATIONS

OF

The American Midland Naturalist

Barr, et al.:
Symposium: Speciation and Raciation
in Cavernicoles $2.50

Bernard:
Cumulative Index,
American Midland Naturalist,
Vols. 1-60 (1909-1958) $4.25

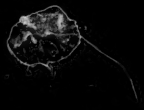
Schuster:
A Monograph of the Nearctic
Plagiochilaceae $4.00

•

Address orders to:

The Secretary

AMERICAN MIDLAND NATURALIST

University of Notre Dame

Notre Dame, Indiana